Effects of Clearcut Logging on Organic Matter and Invertebrate Drift Exported From Headwater Streams in the Interior of British Columbia

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Abstract

We examined streams within clearcuts 1-3 years and 5-7 years post-harvest, and within mature forest (control), to determine the effects of clearcut logging on headwater streams in the interior of British Columbia. We measured fine particulate organic matter (FPOM) concentration during high discharge, dissolved organic carbon (DOC) concentration and DOC composition using spectral ultraviolet absorbance (SUVA) during high and low discharge seasons, and invertebrate drift densities during high discharge. During high discharge, FPOM increased in response to 1-3 year old clearcuts and recovered 5-7 years post harvest, whereas DOC and SUVA did not differ among treatments. During low discharge, DOC did not differ among treatments but SUVA responded positively to new clearcuts indicating an increased proportion of allochthonous DOC. Between seasons, DOC declined in all treatment groups and SUVA increased except in old clearcuts. Invertebrate drift density increased in response to both clearcut groups, and significant responses occurred in seventeen of 52 biotic metrics. Aquatic, terrestrial, Ephemeroptera, Diptera, collector-gatherer and scraper densities responded positively to clearcuts, whereas percent shredders and taxa richness density responded negatively. Densities of common taxa were positively related to FPOM in two cases and did not depend on DOC or harvest history. Our results indicated that invertebrate drift and organic matter exported from small streams were altered 1-7 years post-harvest, and that different responses occurred between the post harvest periods for both abiotic and biotic datasets. With respect to fisheries management, short-term gains in the quantity of resources that sustain the trophic base occurred. The shift in composition of these resources indicates that stability of this export from headwater streams is uncertain.

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The support of my husband, Shon, was critical to pursuing this degree. Thank you for maintaining the lifestyle to which I'm accustomed and for encouraging me! I am grateful to the Greenhalgh's and Mackay's for expressing their interest in my topic. Carol and Bill Greenhalgh lead the way in graduate studies and inspired my curiosity for ecology at a young age. Thank you to Lorne, Mary and Warren Mackay for facilitating my mobile lab.

Prologue

The focus of this study was to determine if streamside clearcut logging affected organic matter and invertebrate drift exported from non-fish bearing, subalpine streams in the interior of British Columbia. Among freshwaters, forested headwater streams have the closest link between terrestrial and aquatic ecosystems, the highest degree of canopy closure, relatively low primary production, and cool water temperatures (Vannote et al. 1980). Small streams have an important element of large woody debris that allows retention of suspended particles and that mediates discharge (Murphy and Meehan 1991). The result of these characteristics is that headwater streams export unique resources that subsidize downstream reaches (Vannote et al. 1980; Wipfli and Gregovich 2002). Decline of allochthonous inputs, increased primary productivity, increased water temperatures and decreased large woody debris occur in the initial years following clearcut logging adjacent to small streams (Brown and Krygier 1970; Webster et al. 1983; Bilby and Bisson 1992; Macdonald et al. 2003a). Consequently, forestry activities alter the characteristics that influence small streams' subsidy to larger streams, yet non-fish bearing streams have the least amount of protection in terms of a no-harvest riparian buffer (Young 2000; Cummins and Wilzbach 2005).

Detritus forms the base of small stream food webs (Fig. 1) and is categorized based on particle size and solubility as coarse particulate organic matter (CPOM >1mm), fine particulate organic matter (FPOM 0.45 μm – 1 mm), and dissolved organic matter (DOM <0.45 μm). DOM comprises the largest pool of organic carbon in freshwaters, an estimated 45-50 % organic carbon by mass (Allan 1995). We used dissolved organic carbon (DOC) as a measurement of DOM and use the terms interchangeably, as is common in the literature. Allochthonous sources of organic matter are leachate of leaf

litter, groundwater, surface flow, and subsurface flow, while autochthonous sources include extracellular release from primary producers, and metabolic by-products of organisms (Lock 1990; Allan 1995). Heterotrophic consumers such as bacteria and fungi are an important means of energy transfer in the food web through their use of DOM. The microbial loop is a pathway whereby energy is essentially recycled among bacteria and successively larger heterotrophs that both consume and exude DOM (Allan 1995).

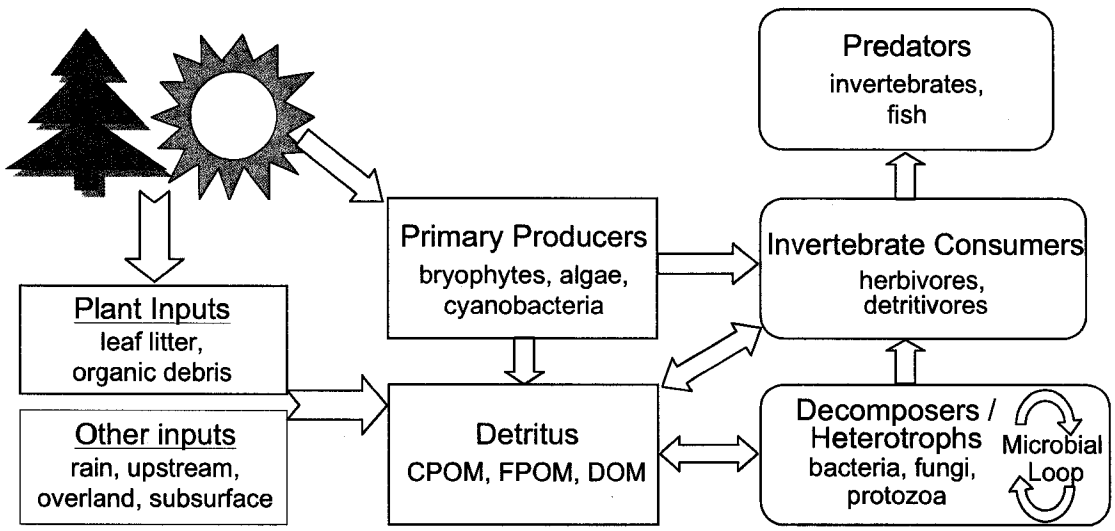

Figure 1. Small stream ecosystem showing energy flow, denoted by arrows. Detritus comprises coarse, fine particulate, and dissolved organic matter (CPOM, FPOM, DOM); rounded boxes show generalized groups of biota (from Allan 1995).

Invertebrates in small streams subsist on detritus directly, or on consumers of detritus. It is useful to categorize macroinvertebrates into functional feeding groups as shredders, collector-gatherers, collector-filterers, scrapers, and predators (Merritt and Cummins 1996). Shredders consume leaf litter and play an important role in breaking down CPOM to FPOM and DOM, after fungi and bacteria decomposers initially colonize the material. Decomposers supply shredders with nutrient value that may surpass that of their substrate (Cummins 1974). Collector-gatherers and collector-filterers directly consume FPOM and DOM, while scrapers consume biofilm, that is a gel matrix of algae,

bacteria, fungi, and detritus that forms on substrates (Giller and Malmqvist 1998). Predators, including groups of macroinvertebrates and fish, consume all of the former groups of consumers.

Reduction of terrestrial litter inputs (Wallace et al. 1997) and reductions in forest cover (England and Rosemond 2004) can affect headwater stream biota by reducing energy transfer through bottom up forces in the food web. In addition to the amount of litter inputs, the quality of organic matter affects energy transfer in the food web by influencing microbial activity (Stelzer et al. 2003) and macroinvertebrates (Hawkins et al. 1982), and predators may rely on a specific composition of invertebrate drift (Bilby and Bisson 1992). The type of organic matter and invertebrates available to predators affects trophic energy transfer because autochthonous derived organic matter and the biota that consume it generally have a higher nutritional quality than allochthonous matter due to lower carbon: nitrogen ratios in the former (Murphy and Meehan 1991).

Under the legislation of the Forest Practices Code of British Columbia Act, implemented in 1995, proximity of logging adjacent to streams was determined by stream categories such as interior versus coastal streams, and stream classifications based primarily on fish presence and bank-full width (Province of B.C. 1995). In 2004, the province implemented the Forest and Range Practices Act, and regulations governing forest harvesting are currently in transition from the Forest Practices Code to the new legislation. The essence of this transition is a shift from basing decisions on broad categories of streams to placing responsibility on forestry professionals to ensure that specific criteria are met as a result of their planning and operations. The goal of this

research is to provide scientific knowledge in a forest type that currently lacks research, and thereby provide tools to strengthen decision-making for resource managers.

Although it is known that clearcut logging can reduce overall organic matter inputs and change their composition (Bilby and Bisson 1992), and alter invertebrate drift (Culp and Davies 1983), the majority of research to date has focussed on interior and coastal fish bearing streams. We identified a knowledge gap for the Englemann spruce subalpine fir (ESSF) biogeoclimatic zone. The ESSF covers 12 % of British Columbia and is the highest elevation forested zone in the southern and central interior of the province (DeLong and Meidinger 2003). Published research in this forest type include clearcut logging effects on hydrology in Colorado (Troendle and King 1985), hydrology research in British Columbia (Winkler et al. 2005), and effects of harvesting on benthic invertebrates in British Columbia (Heise 2001). We chose to examine a dataset in this forest type that also lacks research: the combination of invertebrate drift and organic matter. These variables directly contribute to trophic resources exported from headwater streams. In addition to assessing quantities of these elements, we assessed composition of the drift community, and quality of DOC by measuring the spectral ultraviolet absorbance (SUVA) as an estimate of the proportion of allochthonous DOC. Chapter 1 addresses the abiotic variables, FPOM and DOC, and Chapter 2 examines effects of clearcut logging on invertebrate drift. By examining these variables in headwater streams, this research will expand knowledge for a forest type that is ecologically and economically important, but has previously been little studied.

Chapter 1: Effects of clearcutting on fine particulate organic matter (FPOM) and dissolved organic carbon (DOC) within headwater streams in British Columbia.

Abstract

Fine particulate organic matter (FPOM) and dissolved organic carbon (DOC) form the majority of organic matter transported in headwater streams. We examined effects of clearcutting on FPOM (mg L^{-1}) and DOC, and effects of clearcutting on seasonal shifts in DOC. We measured DOC concentration, and estimated its composition by spectral UV absorbance (SUVA). We selected streams within Englemann spruce – subalpine fir (ESSF) forests in British Columbia in three harvest history treatment groups: "new" 1-3 years post harvest, "old" 5-7 years post harvest, and control streams within mature forests. At each stream, we compared differences between paired sites for FPOM and DOC, and seasonal change relative to high flow for DOC. During high flow, FPOM increased in response to new clearcuts, and recovered 5-7 years post-harvest. DOC concentration and SUVA showed similar trends but were not significant. During low flow, SUVA responded positively to new clearcuts indicating increased allochthonous produced DOC. Seasonally, DOC concentration declined in every treatment and SUVA increased in new clearcuts and controls, but declined in old clearcuts. We suggest that increased photoreactive DOC combined with reduced microbial activity lead to a seasonal increase in the labile pool of DOC in old clearcuts. In new clearcuts, photoreactivity combined with elevated nutrient availability lead to a seasonal reduction in labile DOC. These results indicate increased FPOM, and elevated DOC occurred in new clearcuts that recovered in 5 years post harvest. Responses in DOC composition were only evident 5-7 years post-harvest during the low flow sampling period.

Introduction

Due to the "fish-centric" nature of riparian forest management, small streams that are non-fish bearing often have the least protection in terms of a no harvest riparian buffer (Young 2000; Cummins and Wilzbach 2005). However, fish such as salmonids are seasonally food limited and may receive an important subsidy of organic matter from headwater reaches, especially when considering their cumulative export (Wipfli and Gregovich 2002). It is important to consider cumulative impact because small streams exist in the highest numbers among the continuum of freshwaters and have the closest link between terrestrial and aquatic ecosystems (Vannote et al. 1980). Headwater streams are generally detrital based food webs that rely on a net import of allochthonous organic matter derived from the terrestrial ecosystem. A high degree of canopy closure results in relatively low primary production and cool water temperatures. Small streams also have an important element of large woody debris that allows retention of suspended particles and mediates discharge (Toews and Moore 1982). The result of the combination of these elements is that headwater streams export a unique component of organic matter to subsidize downstream trophic webs.

Streamside timber harvest has varied effects on small stream ecosystems. The main effects include increased nutrients (Gregory et al. 1987), increased primary production (Webster et al. 1983), increased stream temperatures (Brown and Krygier 1970; Macdonald et al. 2003a), and declines of allochthonous inputs (Bilby and Bisson 1992). These responses are predominant in the first decade post harvest and extend until successional vegetation becomes established. In the longer term, reduced recruitment of large woody debris alters stream morphology, leading to declines of woody debris dams,

decreased streambed stability and decreased channel complexity (Gregory et al. 1987). Annual water yields and peak flows generally increase following harvest and can persist for up to three decades post harvest in interior subalpine forests of Colorado (Troendle and King 1985). In combination with changes in stream morphology, increased water yields can lead to increased transport of organic matter in the initial years following harvest, and for decades post harvest (Webster et al. 1983; Troendle and King 1985). Small streams in northern interior forests may respond differently to disturbance (Moore and Wondzell 2005). Yet, among research conducted in the Pacific Northwest Region, which includes the entire province of British Columbia, little research has investigated effects of forestry in the interior of the province. Macdonald et al. (2003a, 2003b) reported increased temperature and suspended sediment in headwater streams of the sub-boreal spruce biogeoclimatic zone and Winkler et al. (2005) reported hydrologic effects of logging in the montane spruce zone in the southern interior of BC. The Englemann spruce subalpine fir (ESSF) biogeoclimatic zone covers 12 % of the province and is the highest elevation forested zone in the southern and central interior of British Columbia (DeLong and Meidinger 2003). Englemann spruce (*Picea englemanni)* is one of the most important commercial species in the interior due to its wood characteristics, and excellent source of pulp (Parish et al. 1996). Despite its ecological and economic importance, research on small streams and their response to forest harvesting is lacking for this forest type.

Removal of riparian vegetation can affect stream ecosystems through organic matter by bottom up processes in the food web. Biota among all trophic levels either directly or indirectly rely on energy input from detritus. Headwater streams quickly

process the largest size category of detritus, coarse particulate organic matter (CPOM), into the smaller particle categories by mechanical action and biotic functions (Winterbourn and Townsend 1991). Fine particulate organic matter (FPOM) is defined as 0.45 μm – 1 mm particle diameter, and dissolved organic matter (DOM) is the category smaller than 0.45 μm (Wotton 1990). Invertebrates and microorganisms directly consume FPOM that is a by-product of fungi conditioning and invertebrate consumption of coarse particles (Suberkropp 1998). Consumers and predators indirectly take up FPOM while consuming primary producers and prey. The combination of FPOM and DOM comprises the majority of organic matter transport in headwater streams, with DOM representing more than 70 % of annual energy flux in streams (Winterbourn and Townsend 1991). DOM comprises the largest pool of organic carbon in freshwaters, and is an estimated 45-50 % organic carbon by mass (Allan 1995). We used dissolved organic carbon (DOC) as a measurement of DOM and use the terms interchangeably, as is common in the literature. DOM is taken up by bacteria, zooplankton and protozoans, and is recycled by these biota through the microbial loop that is thought to form a large part of aquatic food webs (Allan 1995). Fish and macroinvertebrates indirectly consume DOM while preying on biota, and DOM may form a substantial part of their diet. For example, DOM was shown to provide thirty percent of the diet of Limnephilidae caddisfly larvae, a family whose members are generally detritivores (Wotton 1990). Components of DOM play an additional role in the biotic community by attenuating ultraviolet radiation (UVR) that can have harmful effects on fish and invertebrates (Bothwell et al. 1994; Brooks et al. 2005).

DOM substances fall into two general categories: large, complex compounds including humic acids that are refractory and not easily digested, and compounds with low molecular weight such as carbohydrates and free amino acids that are easily assimilated by biota (Wotton 1990). Refractory compounds are generally derived from allochthonous sources of DOM that enter streams from rainfall, run-off, groundwater, and detritus. Low molecular weight compounds tend to be autochthonous, produced by extracellular release from algae, and metabolic waste from stream biota (Allan 1995). In addition to influencing bioavailability of compounds, source of DOM influences the reactivity of compounds when exposed to light, and ability of DOM to attenuate UVR. Allochthonous produced DOM compounds that are large and refractory react on exposure to light to produce low molecular weight, labile compounds, whereas autochthonous DOM tends to be non-photoreactive (Tranvik and Bertilsson 2001). High molecular weight compounds attenuate UVR to a greater degree than low molecular weight components of DOM (Thomas 1997). Thus, allochthonous produced DOM provides a lower quality food resource, tends to be more photoreactive, and provides greater attenuation of UVR than autochthonous produced DOM.

DOM comprises the largest carbon pool in stream food webs, and concentration of dissolved organic carbon (DOC) is used as a measure of DOM (Thomas 1997). Absorbance is measured at various wavelengths in the UV spectrum (280-400 nm) to indicate composition of DOC, and UVR exposure through the water column (Moore 1989; Bothwell 2000; Weishaar et al. 2003; Cory et al. 2004). Spectral UV absorbance (SUVA) is defined as UV absorbance measured in m^{-1} divided by DOC concentration measured in mg L^{-1}, and indicates amount of aromatic carbon (Weishaar et al. 2003).

Aromatic carbons, defined as compounds that contain a benzene ring, are photo- and chemically-reactive, and are primarily associated with humic substances (Thomas 1997). Allochthonous DOC generally contains higher concentrations of UV absorbing compounds, and more aromatic carbons than autochthonous DOC (Tranvik and Bertilsson 2001). Therefore, SUVA can be used to estimate the relative content of allochthonous versus autochthonous DOC. Measuring SUVA at 350 nm indicates both source of DOC and UV exposure in the mid-range of the UVR spectrum.

In terms of organic matter, removal of riparian vegetation may affect stream biota by altering transfer of energy in the food web, or by altering the UVR attenuating effects of DOC. In a stream survey of dissolved organic matter concentrations including 600 streams in British Columbia, ESSF watersheds had among the lowest values, ranging from 1 to 3 mg/L (Bothwell 2000). In northern subalpine forests, DOC levels reach minima during low flow (Burney 1990), and at this time stream biota are most susceptible to the effects of UV radiation (Kelly and Bothwell 2002). Removal of riparian vegetation may affect energy transfer by altering the source of DOC, or by allowing increased photolytic reactions through increased solar radiation. These two effects influence each other as photolytic reactions require DOC primarily made up of allochthonous produced substances.

Our goal was to investigate responses of organic matter to clearcutting within a decade post harvest and to determine if seasonal differences occurred, and if seasonal shifts in organic matter transport responded to clearcutting. We selected the time frame for several reasons. First, the Province of British Columbia implemented the Forest Practices Code in 1995, and in order to compare streams managed under the same

umbrella of legislation and regulations, we selected streams harvested after 1995. Second, we selected a range of years with varying reports of response and recovery for hydrologic and organic matter transport in headwater streams. Third, we investigated a relatively narrow range of years within each clearcut group to minimize variability within treatments. Therefore, we compared undisturbed "control" streams in mature ESSF forests to streams in "new clearcuts" harvested up to three years prior to sampling, and streams in "old clearcuts" harvested up to seven years prior to sampling. We posed three questions with respect to our comparisons among "control", "old clearcuts" and "new clearcuts". First, we evaluated responses of FPOM and DOC to clearcutting during high seasonal discharge. Second, we investigated the seasonal variation in DOC concentration and composition, and third we determined if clearcutting altered seasonal variation in DOC concentration and composition.

Methods

Study Location

We conducted a comparative survey using paired sites located on each selected stream within the ESSF biogeoclimatic zone in the southern interior of British Columbia. Our requirements for selected watersheds within this forest type were that each stream be small, non-fish bearing and that "new" and "old" treatment streams be within clearcuts ranging from one to ten years post harvest. Similar streams within undisturbed forest served as control streams. We also chose to examine two subzones within the ESSF biogeoclimatic zone. Of five candidate study areas identified in conjunction with tenure holders in the region, field reconnaissance determined that two of these areas, Bone Creek and Damfino Creek, met the criteria.

In 2004, we sampled twenty-two streams within the Bone Creek and Damfino Creek study areas (Fig. 2). Ten of the streams were within the Bone Creek study area, located approximately 255 km northeast of Kamloops and situated in the ESSF wet cold subzone Thompson Plateau variant (ESSF wc2; Lloyd et al. 1990). The ESSF wc2 is characterized by 361 mm mean precipitation during the growing season, 782 cm mean annual snowfall, and 1.1 ° C mean annual temperature. Bone Creek is a tributary of the North Thompson River. A waterfall located 150 metres upstream from the mouth of Bone Creek prevents fish passage, leaving the remainder of the watershed absent of fish (FRBC 2001).

The remaining 12 streams were located in the Damfino Creek study area. Damfino Creek is located approximately 260 km southeast of Kamloops within the ESSF dry cold subzone, Okanagan Highlands variant (ESSF dc1; Lloyd et al. 1990). The ESSF dc1 is characterized by 261 mm precipitation during the growing season, 635 cm mean annual snowfall and 2.0 ° C mean annual temperature (Lloyd et al. 1990). Streams in this study area were within two watersheds, Damfino Creek and Two John Creek, which are separated by approximately ten kilometres. Damfino Creek flows into the Kettle River, and Two John Creek flows into the West Kettle River; both rivers are tributaries of the Columbia River. A waterfall located 561 m from the mouth of Damfino Creek prevents fish passage to the upstream reaches, and barriers restrict fish migration in the upper reaches of Two John Creek where sample streams were located (FRBC 2000).

All streams selected in this study fall under the S6 stream classification (Province of BC 1995), which includes non-fish bearing streams no greater than 3 m bank-full width. Cutblocks selected in this study ranged in size from 20 to 95 ha and contained up

to 24 identified S6 streams within one block. Best management practices prescribed retention of the most windfirm 5 % of codominant conifers within 20 m of the channels of two streams for every 40 ha of harvest area, and full retention of non-merchantable vegetation within 5 m (Province of BC 1995). All treatment streams were nearly to completely void of conifers in their riparian zones, and where conifers remained they were early seral and sparse. A portion of streams in each treatment had non-merchantable vegetation left in the riparian zone that comprised deciduous species such as alder (*Alnus tenufolia)* and rhododendron (*Rhododendron albiflorum)*. The primary logging method used within Damfino study area streams was conventional grapple skidding, while high lead yarding was common in Bone Creek study area due to steeper topography.

Although this study was not designed to quantify or evaluate the effects of slash, organic matter left in or adjacent to streams is considered an important influence on stream responses to clearcut logging. Our observations were that slash presence was variable among clearcut streams ranging from very little slash present immediately adjacent to the channel, to high amounts of slash that covered the stream channel. Figure 3 shows examples of slash presence representative of the intermediate amount of slash, not completely covering the stream but present in the riparian zone and the channel. The specific influence of slash was not tested in this study as the objective was to evaluate effects of the end result from clearcut harvesting, regardless of site specific differences in logging operations.

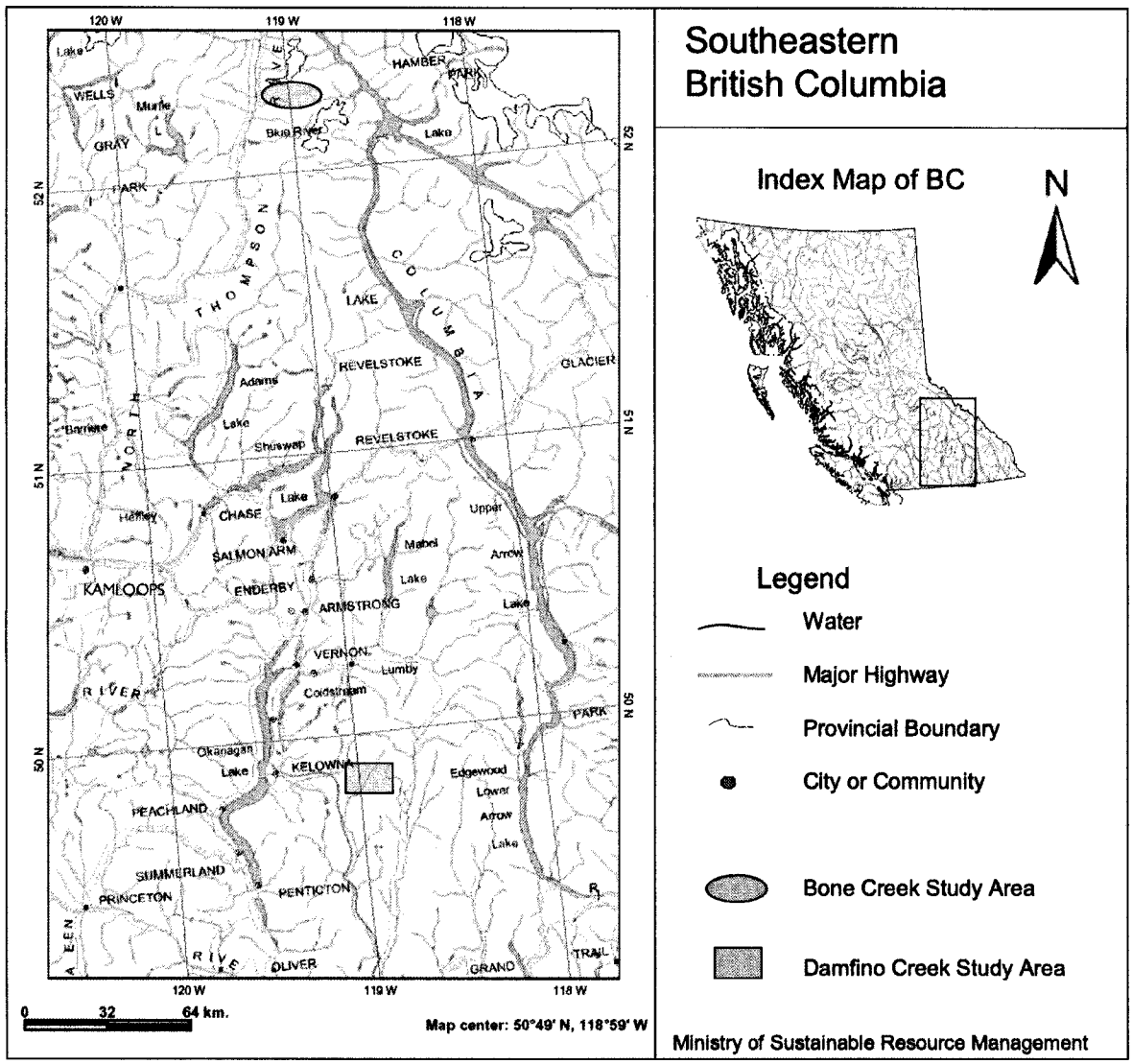

Figure 2. Location of study areas within British Columbia.

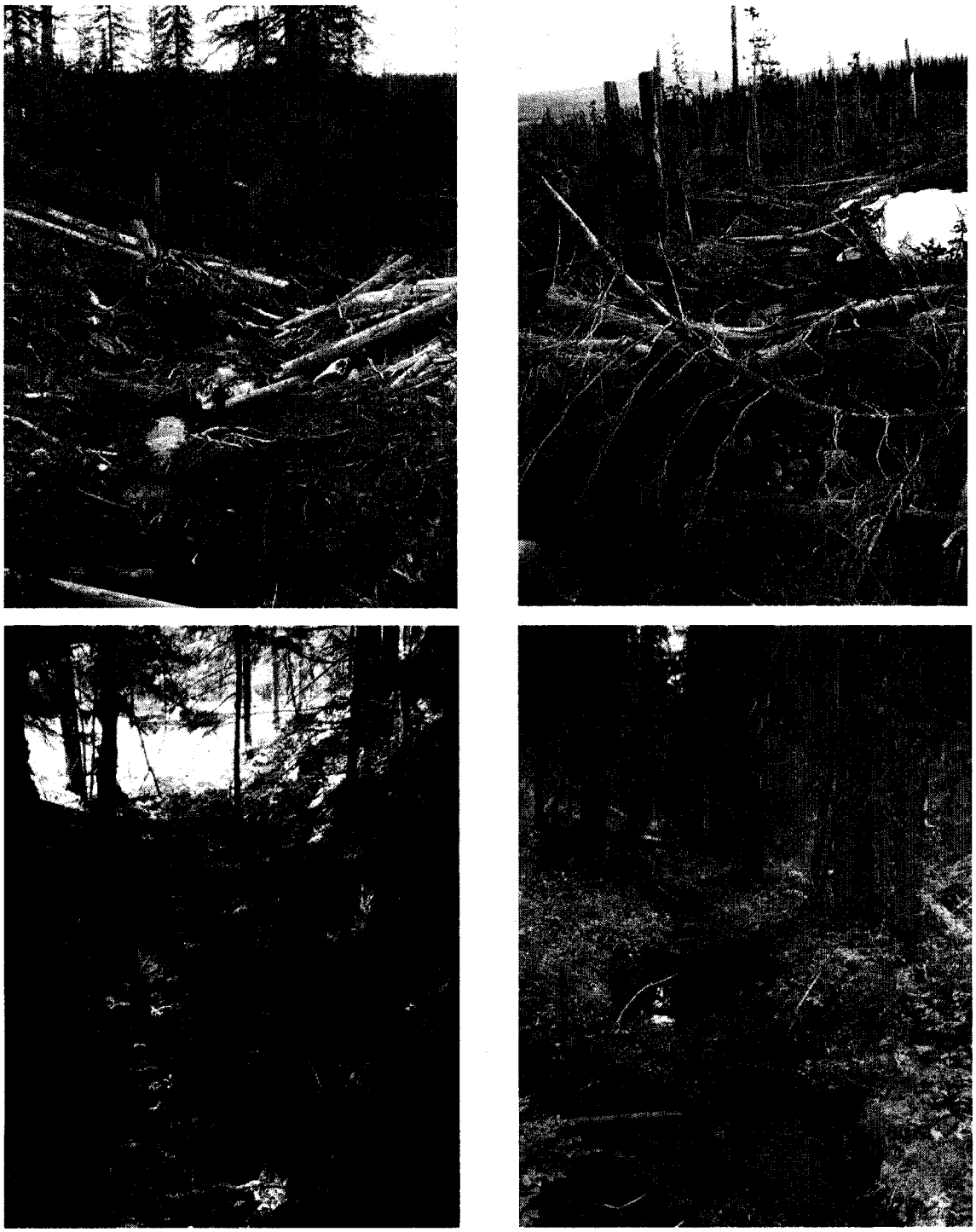

Figure 3. Two examples of slash in proximity to streams in this study compared to two control streams; all photographs were taken in 2004. Top left photograph is stream 215 logged in 2003, and top right photograph is stream 206 logged in 1998; both streams are within Damfino Creek study area. Bottom left photograph is control stream 013 at Bone Creek study area, and bottom right photograph is control stream 203 at Damfino Creek study area.

Experimental Design

Selected streams fell into one of three treatment categories: "control" streams within undisturbed mature forest, "new" streams within clearcuts 1-3 years post harvest, and "old" streams within clearcuts 5-7 years post harvest. The minimum distance that a stream flowed through its associated cutblock was 300 metres at Bone Creek and 250 metres at Damfino Creek. Therefore, this minimum distance separated the downstream site from the upstream forest edge, and an additional 50 metres separated the forest edge from the upstream site (Fig. 4). The same distances separated control stream paired sites located at elevations and physical characteristics representative of treatment streams. Streams served as replicate sampling units to avoid issues of pseudoreplication (Hurlbert 1984). We considered differences between paired sites of control streams as the reference level, and compared the reference level to differences between paired sites of clearcut treatments. This is similar to a before-after control-impact design, and is effective to detect responses to disturbance (Underwood 1994).

We addressed potentially confounding variables by judicious site selection and timing of sampling. We maintained a consistent slope distance between paired sites in order to reduce variability associated with effects that may occur as a function of reach length. We excluded streams if they had insufficient flow, if they flowed through a known disturbance upstream from the selected clearcut, and if they contained a riparian buffer of timber. To avoid the additional influence of roads, we excluded streams crossed by active or decommissioned roads larger than skid trails within or above the paired sites. We selected reference streams with a range of physical characteristics representing those of treatment streams.

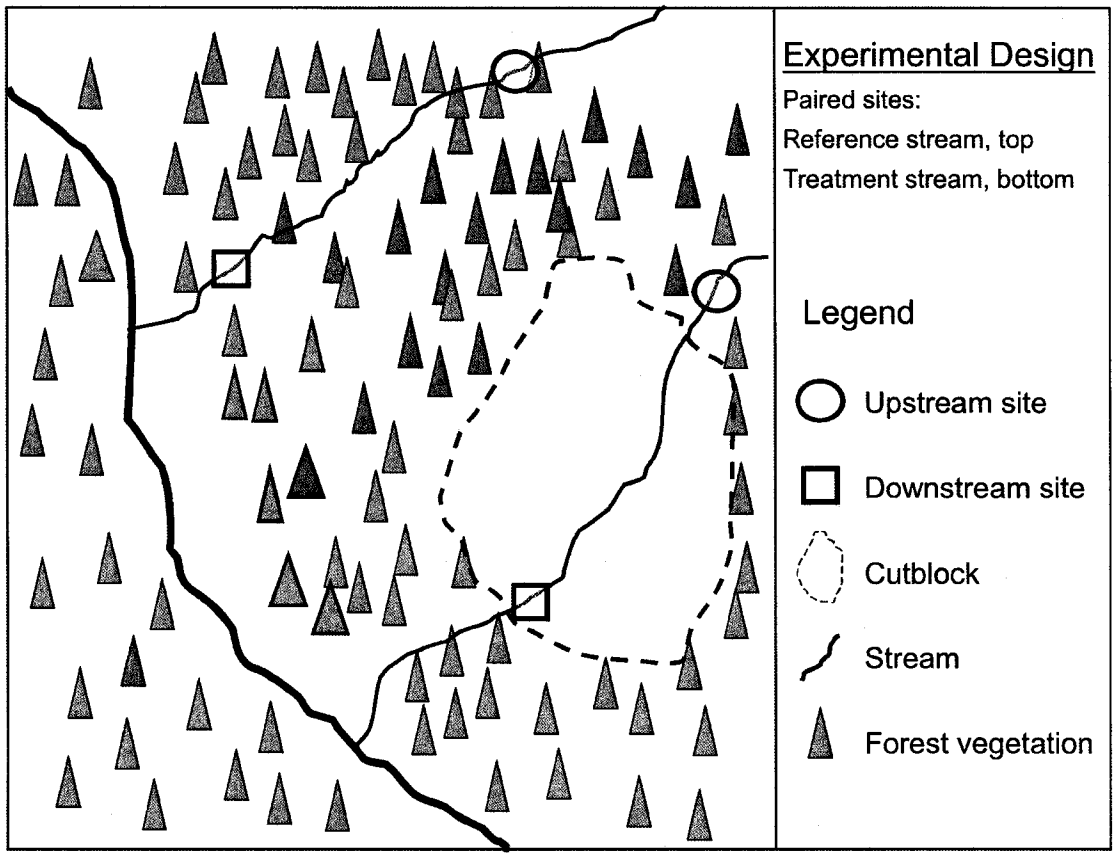

Figure 4. Schematic diagram showing experimental design.

Timing of sampling influences organic matter export rates due to seasonal and diel periodicity, and discharge pulses. Sampling dates corresponded with high and low periods according to Water Survey of Canada archived data for the study areas (Fig. 5). We commenced sampling at the same time each day, with downstream sites in the morning followed by upstream sites in the afternoon. We did not sample within 24 hours of heavy rainfall. Treatments were sampled alternately within each sampling period, as opposed to sampling all control streams then all clearcut streams, to avoid bias from seasonal fluctuation through our sampling timeframe.

From June 18 - July 23, 2004 we sampled paired sites on 12 streams at Damfino Creek, and from August 12 - 29 we sampled paired sites on 10 streams at Bone Creek.

We sampled an additional four unpaired sites consisting of two "old" and two "control" treatments at Bone Creek because paired sites were not available that met our criteria. During the low flow period, we did not sample any upstream sites in the Bone Creek study area due to time constraints, and data collection was not possible at stream 002 due to access restriction from a landslide. At Damfino Creek, we did not conduct low flow sampling at the upstream site of stream 210 that was entirely dry.

Each stream was assigned an identification number in chronological order of sampling with the leading digit representing the study area. All physical attributes were measured during the high flow period (Table 1). Water temperature data were successfully collected at 18 sites for periods ranging from one to seven days surrounding the sample date of each stream. Water temperature data were collected for reference of physical stream characteristics and were not entered into analysis, whereas the remaining physical data were used in analysis.

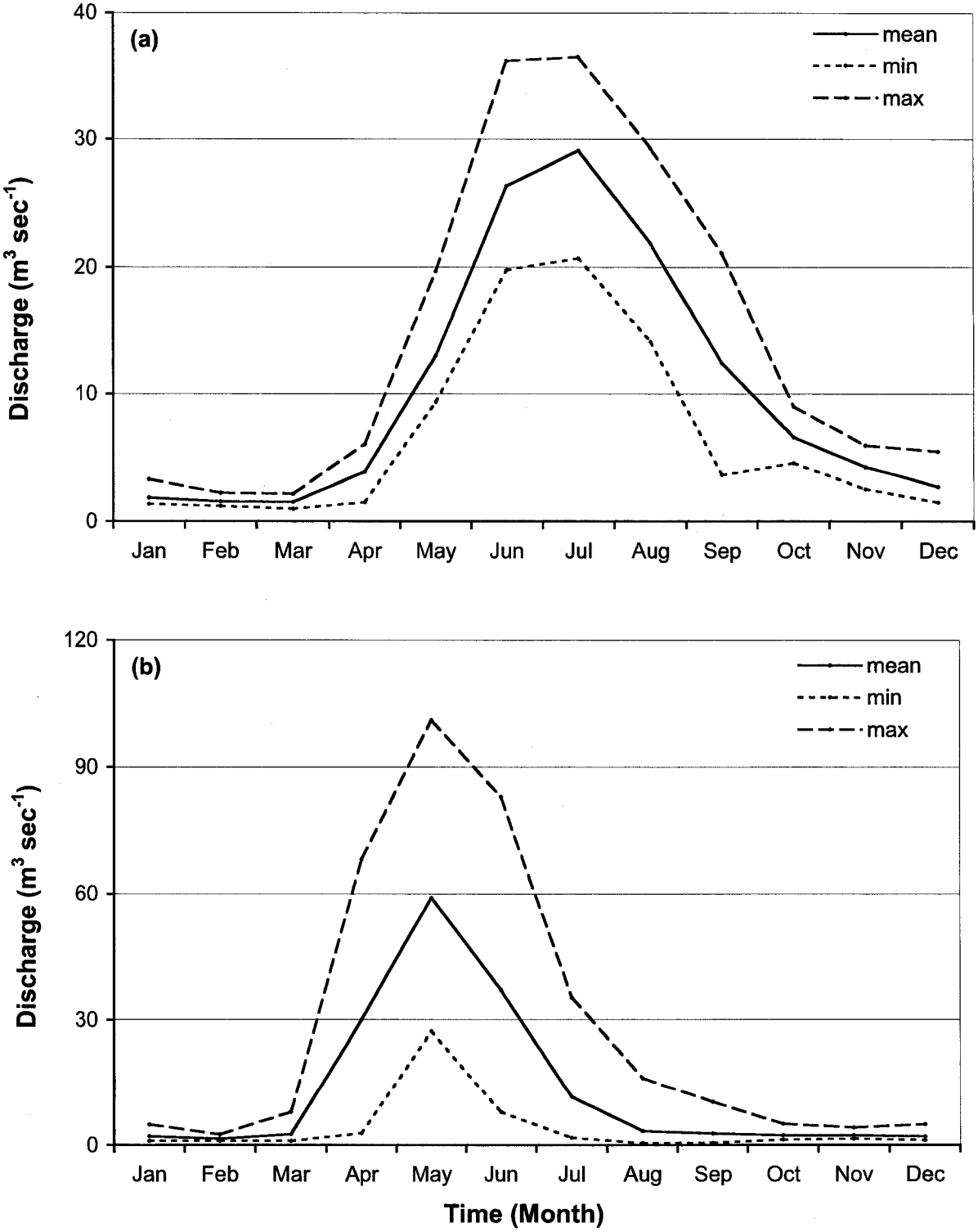

Figure 5. Hydrographs for (a) Bone Creek and (b) West Kettle River showing mean daily discharges. (Water Survey of Canada, 2006).

Table 1. Physical characteristics and sampling dates of study streams sampled in 2004 within the Bone Creek and Damfino Creek study areas.

Stream ID [a]	Treat-ment	Year logged	Canopy closure (%) [b]	Discharge (L sec^{-1})	Bank-full width (m)	Stream gradient (%)	Aspect	Elevation median [c] (m)	Water Temp. [d] Min (° C)	Water Temp. [d] Max (° C)	Date sampled High Flow	Date sampled Low Flow
Bone Creek												
005	Control	-	25	5.46	0.47	35	W	1184	9.8	14.8	14-Aug	4-Oct
012	Control	-	78	12.38	2.72	34	E	1131	8.9	12.3	24-Aug	4-Oct
013	Control	-	94	2.39	2.13	32	SE	1297	5.7	7.6	19-Aug	4-Oct
025	Control	-	52	4.28	0.61	32	NE	1671	7.9	9.9	27-Aug	5-Oct
021	New	2003	0	1.31	0.85	41	S	1536	9.9	11.8	13-Aug	4-Oct
023	New	2003	0	0.59	0.68	31	S	1845	6.1	12.3	13-Aug	4-Oct
002	New	2002	42	0.63	0.94	57	E	1453	n.d.	n.d.	25-Aug	n.d.
027	New	2001	59	3.42	1.03	65	SW	1543	8.8	9.2	29-Aug	4-Oct
010	Old	1999	0	0.43	2.50	58	N	1262	9.5	11.6	12-Aug	4-Oct
011	Old	1998	0	1.66	1.00	33	NE	1171	9.2	11.8	26-Aug	4-Oct
Damfino Creek												
203	Control	-	77	4.16	1.63	4	SW	1566	4.6	12.0	26-Jun	31-Aug
208	Control	-	5	4.29	0.71	18	S	1592	8.4	8.6	9-Jul	31-Aug
209	Control	-	73	4.11	1.56	23	NW	1820	6.5	16.0	11-Jul	31-Aug
213	Control	-	84	1.17	1.04	12	NE	1682	n.d.	n.d.	21-Jul	31-Aug
201	New	2003	63	19.04	0.86	7	SE	1547	5.5	12.0	18-Jun	30-Aug
205	New	2003	17	3.77	1.02	14	N	1660	7.3	11.2	29-Jun	31-Aug
207	New	2003	55	5.63	0.76	14	SE	1730	6.1	19.9	10-Jul	31-Aug
215	New	2003	57	1.47	1.62	16	NE	1652	n.d.	n.d.	23-Jul	31-Aug
206	Old	1998	92	1.41	1.01	9	E	1873	6.4	16.7	30-Jun	31-Aug
210	Old	1998	18	0.18	1.30	24	N	1825	7.4	10.0	13-Jul	31-Aug
211	Old	1998	39	0.92	0.76	27	W	1830	6.2	8.5	14-Jul	31-Aug
202	Old	1997	45	2.69	0.86	8	W	1695	n.d.	n.d.	25-Jun	31-Aug

Note: Attributes measured during high flow sampling period with multiple measurements at each site. Stream average values are presented with the exception of canopy closure, which are given for downstream sites for comparison of logged versus old growth. (n.d. = no data).

[a] All streams are unnamed; therefore, each stream was assigned a number with the leading digit indicating study area

[b] Canopy closure represents percentage of cover measured by densiometer 1 m above ground at downstream sites

[c] Represents the median elevation between downstream and upstream paired sites

[d] Water temperaure logged hourly over at least 24 hours during high flow sampling date of each stream

Data Collection

We recorded physical characteristics at each site during high flow sampling including canopy closure, discharge, bank-full width, stream gradient, aspect, and elevation. At two locations for each site we used a densitometer held 1 metre above ground, facing four directions to determine canopy closure (Lemmon 1956). We measured discharge by recording the time to fill a large container of known volume at least six times throughout sampling and obtaining the average (Gore 1996). We measured bank-full width at three locations, and gradient and aspect at each site using a clinometer and compass. We obtained elevation and UTM coordinates with GPS at each site location, and verified elevation using topographical maps. Temperature loggers were placed in streams at each site surrounding the high flow sampling period and recorded hourly water temperature over at least 24 hours.

We collected fine particulate organic matter (FPOM) samples during the high discharge period only, and dissolved organic matter (DOM) samples during two seasons. At each downstream and upstream site we triple rinsed three 11 L carboys using stream water, and filled each carboy using a sieve to remove particles greater than 1 mm in diameter. Using vacuum filter apparatus with hand pumps, we filtered the water using pre-ashed, pre-weighed glass fibre filters of nominal pore size 0.7 μm (Whatman GFF) in triplicate. From each carboy, we filtered four litres of water or an amount sufficient to leave a visible layer, and retained each filter in a pre-ashed tinfoil envelope within a sealed plastic bag. At the end of each day, we froze the samples and kept them frozen until analysis. In the laboratory, we processed the filters and used gravimetric analysis as

described in Wallace and Grubaugh (1996) to determine ash-free dry mass (mg L^{-1}) of FPOM.

We retained the remaining filtrate of each sample in 60 mL amber glass bottles and kept samples refrigerated for subsequent DOC analysis. We used a total carbon analyzer (Model V SCH, Shimadzu Corporation; Kyoto, Japan), using the non-purgible organic carbon method, to obtain DOC concentrations in parts per million or mg L^{-1}. We measured the absorbance of each sample at 350 nm (25° C) using a Cary 50 spectrophotometer (Varian Incorporated; Palo Alto, California, USA). The spectral ultraviolet absorbance ($SUVA_{350}$) of each sample was calculated using absorbance divided by DOC concentration (Weishaar et al. 2003).

Data Analysis

We used discriminant analysis to test for natural patterns among streams using mean discharge, bank-full width, stream gradient, aspect and elevation of each stream as independent variables. If physical characteristics did not predict group membership among treatments, then we assumed that responses of organic matter were due to logging or season rather than natural variability among subject streams. The physical stream variables were log transformed in order to achieve equal population covariances, to reduce the influence of outliers, and to meet the assumption of multivariate normality required for discriminant analysis (Tabachnick and Fidell 1989).

For each response variable, FPOM concentration, DOC concentration, and $SUVA_{350}$, we used site means to determine effect as the difference between paired sites relative to the upstream reference site (Equation 1). A negative effect indicated the variable decreased after flowing through the clearcut or between paired sites, whereas a

positive effect indicated the variable increased. Control stream effects served as the base condition to compare against treatment stream effects.

$$Effect = \left[\frac{ds - us}{us}\right] \times 100 \qquad \textit{Equation 1}$$

Where ds = downstream site average, us = upstream site average.

All data were checked for normality and homoscedasticity. FPOM effect required a $Log_{10}(x+1)$ transformation to meet the assumption of normality; the remaining variables did not require transformations. Data are presented untransformed for ease of interpretation.

To assess the appropriateness of pooling data from the two study areas, we used a two-way ANOVA with treatment and watershed as fixed factors. If there was not a significant interaction between watershed and treatment ($p>0.05$), then analysis proceeded using pooled data and single factor ANOVA was used to detect differences among treatments for the remaining variables with *a priori* contrasts. The contrasts were chosen to detect differences between the following groups: *i)* control and old clearcuts, *ii)* control and new clearcut streams, and *iii)* old and new clearcut streams.

We first assessed seasonal differences in DOC concentration and $SUVA_{350}$ using a paired t-test. This approach evaluated seasonal differences by comparing two measurements taken at identical sites. We used all upstream and downstream sites that had measurements for both seasons (n=36). Additional sample size was possible for this analysis because the unpaired downstream sites were included in the paired t-test but not in downstream-upstream effect (Equation 1) analysis.

The effect between sampling periods gave differences between paired site measurements repeated during high and low flow, relative to high flow values (Equation

2). In this second approach, we used a subset of the paired t-test data due to Bone Creek sites lacking upstream low flow data. The purpose of this approach was to detect if seasonal response depended on treatment for DOC concentration and $SUVA_{350}$. We used a two-way ANOVA with study area and treatment as fixed factors. If study area did not contribute to the general linear model, we then used a one way ANOVA with treatment as the factor and *a priori* contrasts as specified above to determine if season effect depended on treatment.

$$Effect = \left[\frac{LF - HF}{HF}\right] \times 100 \qquad \textit{Equation 2}$$

Where HF = high flow site average, LF = low flow site average.

Results

Stream Physical Characteristics

Discriminant analysis found that discharge, bank-full width, stream gradient, aspect and elevation did not predict group membership to the three treatment types (Wilks' $\lambda = 0.45$, $p=0.19$). This supported our assumption that effects found to differ among treatment type are due to logging or season rather than natural variability, with respect to the physical attributes measured (Fig. 6a). Average canopy closure at downstream sites of control streams was 61 %, and was reduced to 32 % and 37 % on average at old and new clearcut sites respectively (Fig. 6b). *A priori* contrasts did not detect any differences between treatment groups ($p>0.05$). ANOVA also did not detect a difference in canopy closure among treatment streams ($F_{2,19}=1.9$, $p=0.18$). Canopy closure values varied highly within treatments and overlapped between control and clearcut streams. This was due to numerous clearcut streams being highly shaded with dense early successional vegetation, and several control streams having an understory

comprising herbaceous species that were less dense than that of early successional vegetation.

Pooling Study Areas

Table 2 summarizes DOC concentration, $SUVA_{350}$, and FPOM concentrations by treatment and study area for upstream and downstream sites. The two way ANOVA analyses showed that study area (Bone Creek or Damfino Creek) did not significantly contribute to the model used to discern treatment responses in FPOM, DOC and $SUVA_{350}$ effects (p=0.16, 0.10, 0.85), nor were there significant interactions between treatment and study area for the three variables (p=0.15, 0.22, 0.50). Therefore, we pooled data from both study areas and compared mean effect among treatments including all 22 streams.

Treatment Response

During the high flow period, FPOM differed among treatments ($F_{2,19}$=3.6, p=0.048). FPOM responded positively to new clearcuts compared to control streams (p=0.032) and old clearcut streams (p=0.036, Fig.7). Contrasts and ANOVA did not detect differences in DOC ($F_{2,19}$=1.7, p=0.20) or $SUVA_{350}$ ($F_{2,18}$=0.69, p=0.52) among treatments (Fig. 7). Data were missing for one control sample for $SUVA_{350}$ measurements. Effects for streams 002 and 023, both within new clearcuts, were extreme at 381 % and 196 % respectively. Excluding these outliers changed the mean of the new treatment from 75.7 % (SEM = 49.8 %) to 4.75 % (6.21 %) and the result of the ANOVA test to $F_{2,17}$=0.008, p=0.992. One of these streams, 023, was also an outlier for FPOM effect; however, exclusion of this stream did not alter the significances for FPOM.

During the low flow period, DOC did not differ among treatments (Fig. 8, ANOVA: $F_{2,10}$=0.52, p=0.61; contrasts: p>0.05). $SUVA_{350}$ differed among treatments

($F_{2,10}$=5.9, p=0.027), with increased values between new clearcut sites (p=0.009) and pooled clearcut sites (p=0.022) compared with controls (Fig. 8).

Seasonal Response

There were seasonal differences for DOC concentration (t_{38}= 4.2, p<0.001) and $SUVA_{350}$ (t_{36}=-2.6, p=0.012). In Figure 9 it is clear that DOC declined in each treatment within both study areas in the low flow compared to high flow season. $SUVA_{350}$ seasonal differences followed similar trends in each study area, with seasonal decline in old clearcut streams only (Fig. 9). Mean DOC concentration decreased by 19 % from high to low flow, and mean $SUVA_{350}$ increased by 19 % at low flow (Fig.10).

Treatment x Seasonal Response

Season effect did not vary among treatments for DOC (Fig. 11, ANOVA: $F_{2,20}$=0.98, p=0.40; contrasts: p>0.05). Although ANOVA did not detect differences in $SUVA_{350}$ among treatments ($F_{2,20}$=3.4, p=0.057), *a priori* contrasts showed that $SUVA_{350}$ seasonal effect in old clearcuts differed from both control streams (p=0.029) and new clearcut streams (Fig. 11, p=0.041).

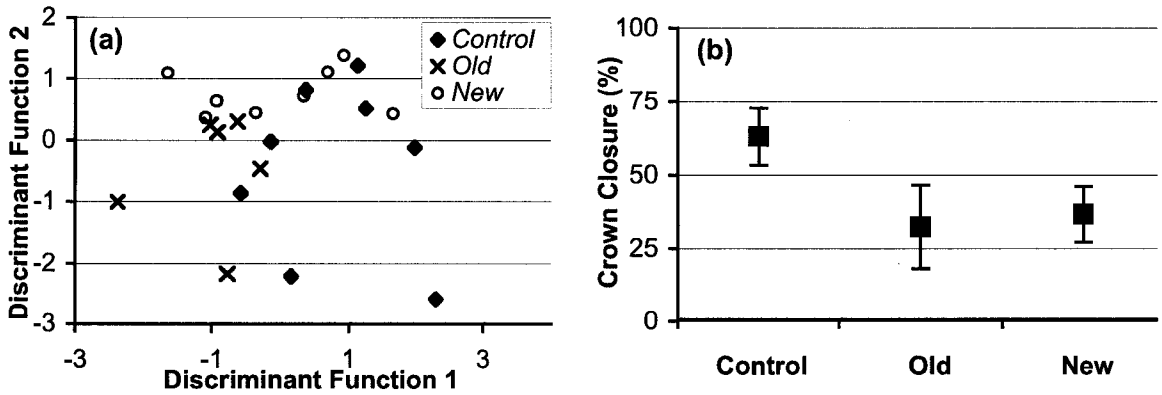

Figure 6. (a) Two discriminant functions describe stream abiotic characteristics and do not predict group membership to the three treatments (Wilks' λ=0.45, p=0.19). (b) Mean crown closure at downstream sites does not differ among treatments (p=0.12); error bars represent SEM. Control n=8, old clearcuts n=6, new clearcuts n=8.

Table 2. Mean DOC concentration (mg/L), specific UV absorbance ($SUVA_{350}$, L m^{-1} mg^{-1}) and FPOM concentration (mg/L) by treatment and study area summarized for downstream and upstream sites among treatments. Standard errors of the mean are given in parentheses.

	Bone Creek			Damfino Creek		
	Control	Old	New	Control	Old	New
Downstream Sites						
DOC: High flow	3.09 (0.77)	4.92 (0.72)[a]	5.09 (1.11)	5.28 (0.33)	5.30 (0.50)	5.53 (0.51)
DOC: Low flow	2.12 (0.72)	4.77 (0.11)[a]	3.53 (0.68)[b]	5.09 (0.44)	5.11 (0.41)	4.49 (0.36)
SUVA: High flow	0.69 (0.09)	0.90 (0.01)[a]	1.08 (0.11)	0.87 (0.08)	1.01 (0.68)	0.88 (0.11)
SUVA: Low flow	0.99 (0.05)	0.85 (0.02)[a]	1.42 (0.11)[b]	0.91 (0.05)	0.92 (0.12)	1.03 (0.96)
FPOM: High flow	1.24 (0.58)	1.75 (0.75)[a]	2.70 (0.69)	0.33 (0.11)	0.32 (0.06)	0.41 (0.12)
Upstream Sites						
DOC: High flow	2.89 (0.46)	3.81 (0.24)[a]	3.74 (1.60)	5.10 (0.34)	5.96 (0.40)	5.30 (0.53)
DOC: Low flow	-	-	-	4.58 (0.32)	5.24 (0.66)[b]	4.37 (0.13)
SUVA: High flow	0.81 (0.13)	1.08 (0.07)[a]	0.96 (0.18)	0.93 (0.10)	0.94 (0.14)	0.84 (0.10)
SUVA: Low flow	-	-	-	1.14 (0.16)	0.94 (0.14)[b]	0.87 (0.07)
FPOM: High flow	0.90 (0.11)	3.50 (1.51)[a]	0.74 (0.21)	0.69 (0.36)	0.36 (0.10)	0.31 (0.07)

Note: There are four streams in each category except where noted by [a] n=2; [b] n=3.

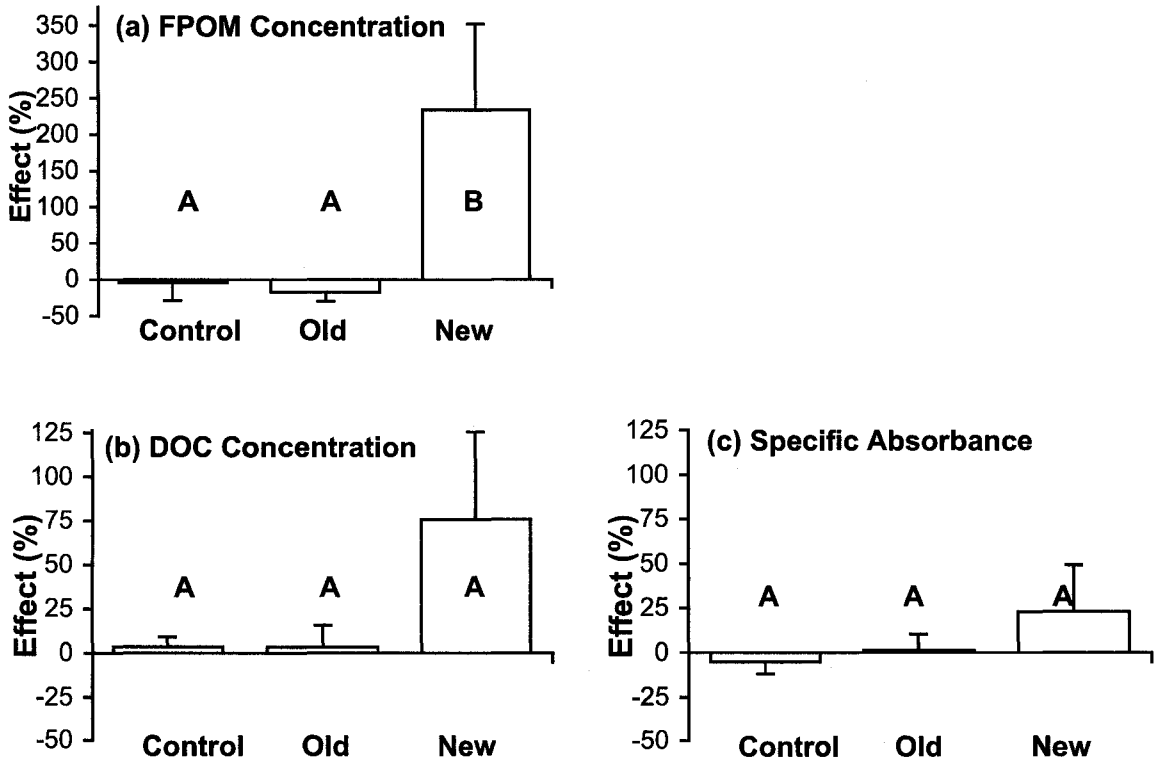

Figure 7. Columns show mean effect for (a) FPOM, (b) DOC and (c) specific absorbance ($SUVA_{350}$) among treatments during high flow; error bars denote SEM. Positive effect indicates an increased value, whereas negative effect indicates a decrease from upstream to downstream sites. Treatment means with common letter do not differ significantly ($p>0.05$). (Control n=8, Old n=6, New n=8).

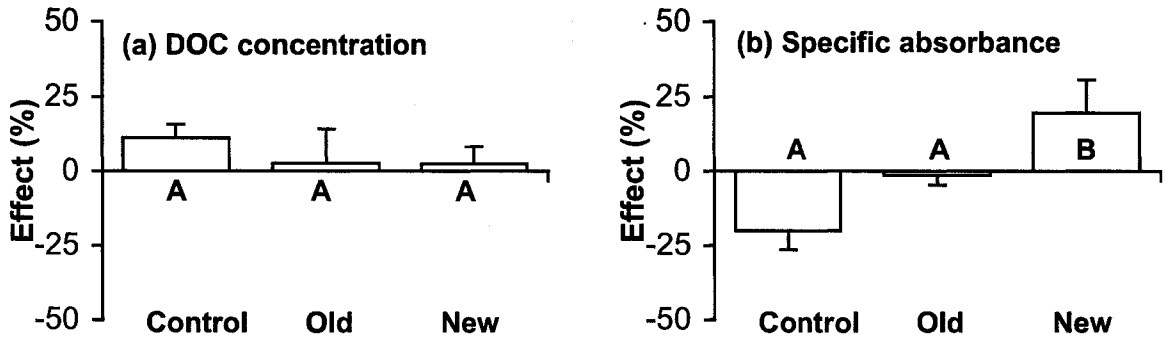

Figure 8. Mean effect for (a) DOC concentration and (b) specific absorbance ($SUVA_{350}$) among treatments during low flow season; error bars denote SEM. Positive effect indicates an increased value, whereas negative effect indicates a decrease from upstream to downstream sites. Treatment means with common letters do not differ significantly ($p>0.05$).

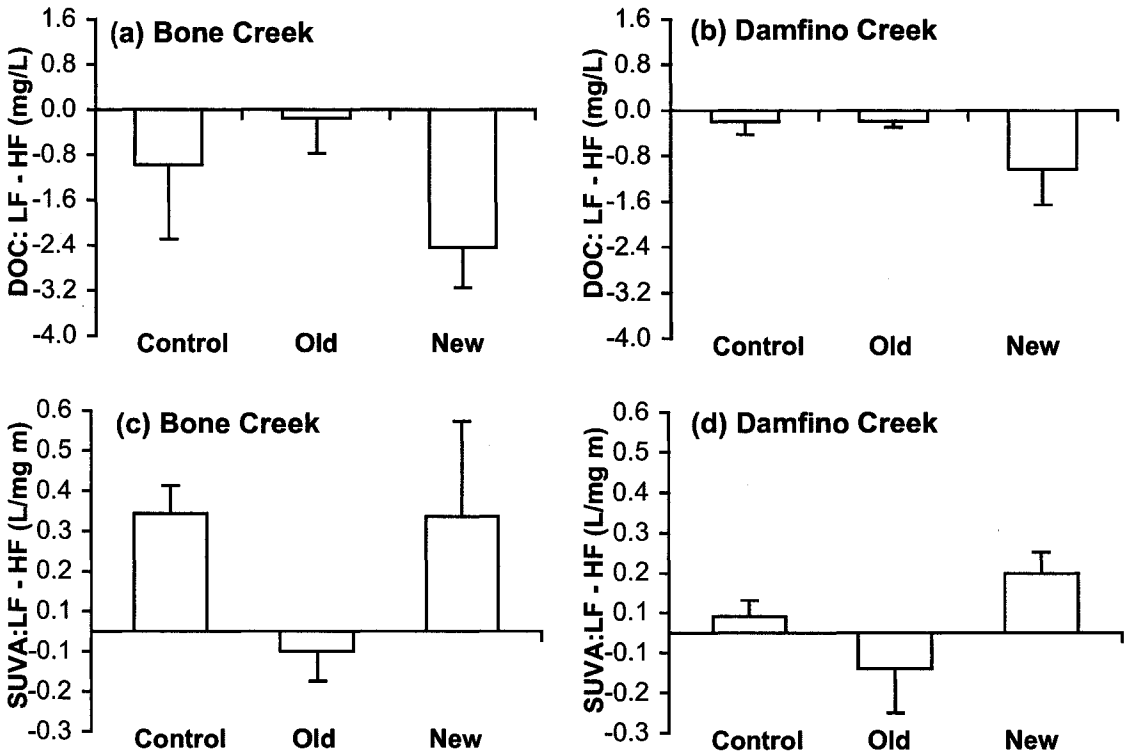

Figure 9. Mean seasonal differences at downstream (impacted) sites for DOC concentration at (a) Bone Creek, (b) Damfino Creek; and for specific absorbance, $SUVA_{350}$ at (c) Bone Creek and (d) Damfino Creek. Error bars denote SEM. DOC decreased during low flow in every treatment indicated by negative values, whereas $SUVA_{350}$ tended to increase from high to low flow. Bone Creek: Control n=4, Old n=2, New n=3. Damfino Creek: Control n=4, Old n=4, New n=4.

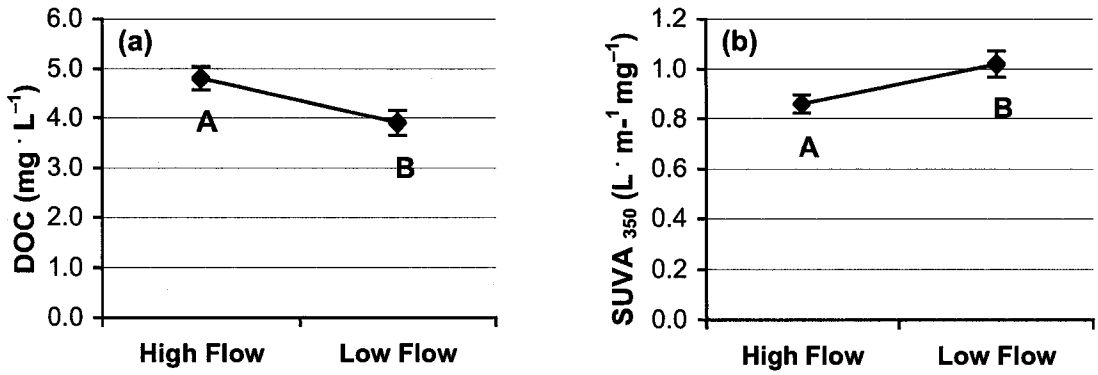

Figure 10. (a) Mean DOC concentration and (b) mean specific absorbance ($SUVA_{350}$) during high flow and low flow sampling. Error bars represent SEM. Treatment means with a common letter do not differ significantly ($p>0.05$). (DOC n=39; $SUVA_{350}$ n=37).

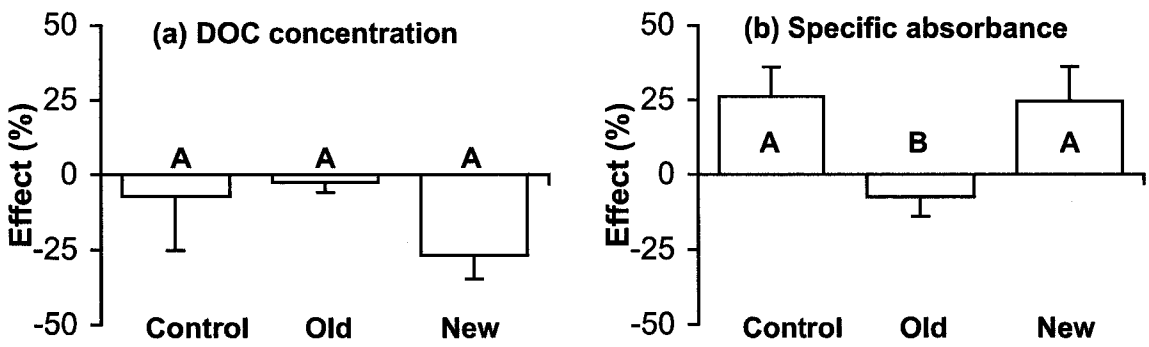

Figure 11. Mean seasonal effect among treatments for (a) DOC concentration and (b) specific absorbance ($SUVA_{350}$); error bars denote SEM. DOC concentration decreased from high to low flow indicated by negative effect values. $SUVA_{350}$ increased in control and new, and decreased in the old clearcut treatment. Control n=8, Old n=6, New n=7.

Discussion

Treatment Response

FPOM concentration increased in streams flowing through new clearcuts compared with control and old clearcut streams. This is in agreement with results from previous work. In North Carolina, disturbed streams contained higher particulate organic matter (POM) initially following clearcut logging, and recovered within four years (Webster et al. 1983). Macdonald et al. (2003a) found increased levels of suspended

sediments following harvesting activities in the sub-boreal spruce zone in central BC that recovered to pre-harvest conditions within three years following harvest. Our results were also consistent with data collected a year previous to this study in Bone Creek (Greenhalgh and Heise 2004). Our findings indicate that FPOM in the water column increases 1-3 years post harvest in response to removal of riparian vegetation, but returns to reference levels in the period 5-7 years following harvest.

DOC concentrations we observed fall in the lower range of comparable headwater streams reported in the literature. Reported values include a peak flow average of 7.0 mg/L (Colorado, Hood et al. 2005), a range of 5.3-17.6 mg/L (Colorado/Montana, Brooks et al. 1999) and 3.2-7.2 mg/L (Quebec, Eckhardt and Moore 1990). In the current study, DOC high flow treatment means fell between 2.89–5.96 mg/L, and low flow means were 2.12–5.24 mg/L. Biota within streams containing DOC in this range are most vulnerable to UV exposure through either increased UVR or decreased DOM (Kelly and Clare 2001; Kelly et al. 2003). Subalpine aquatic food webs may be particularly susceptible to global or regional increased UVR because light penetration increases with elevation due to atmospheric thinning, reduced topographic shading and longer daylength (Williamson et al. 1996). The results of this study support a prior survey (Bothwell 2000) that small streams in the ESSF contain DOC at threshold concentrations in terms of detriment to biota if UVR increased, or if DOM input decreased.

Although differences were not significant during high flow, DOC concentration tended to increase within streams flowing through new clearcuts (Fig. 7b). $SUVA_{350}$ showed a similar non-significant trend during high flow. Although low flow DOC concentration effects did not differ among treatments, $SUVA_{350}$ effect differed indicating

elevated allochthonous input in response to new clearcuts. Our findings that DOC concentration did not respond, or only slightly responded to disturbance are comparable to other findings from headwater streams. Kreutzweiser et al. (2004) found no change in DOC concentrations, and increased DOC export that recovered two years post harvest in selective harvesting after up to 89 % removal of basal area. Moore and Jackson (1989) found 1-4 year old cutblocks had little effect on DOC export. Our $SUVA_{350}$ results concur with the response reported by Hood et al. (2006) that as DOC concentrations increased during high run-off, $SUVA_{254}$ increased 35 % in clearcut watersheds, and only 10 % in reference watersheds. An investigation of two headwater streams in Arkansas found higher refractory pools of DOC in an agriculturally impacted stream compared to an undisturbed stream (Ziegler and Brisco 2004). Burney (1990) proposed two pathways that cause increased DOC concentrations during rising water; flush of the accumulation of microbes and organic matter under snow pack, and run-off from mineral soil-derived refractory compounds. The first pathway dominates snow-fed streams and the amount of labile DOC derived is positively related to amount of heterotrophic activity during winter (Brooks et al. 1999). We suggest that elevated organic matter adjacent to new clearcuts influenced the DOC flush during run-off by supplying increased allochthonous compounds compared with control streams.

Seasonal Response

The allochthonous influence on DOC during high flow in new clearcuts was also found during low flow, but this terrestrial signal was greater during low flow. DOC concentrations decreased between high and low flow while the portion of refractory compounds ($SUVA_{350}$) increased. Seasonal reductions in DOC concentration agree with

many previous studies in headwater streams and are attributed to highest discharge periods providing maximum inputs of DOC (Tate and Meyer 1983; Moore 1989; Brooks et al. 1999; Kiffney et al. 2000; Hood et al. 2003). During high discharge periods, DOC is derived primarily from terrestrial sources leading to high refractory composition unless mediated by heterotrophic activity under snow pack. Previous work on seasonal shifts in DOM composition found differing results depending on dominating sources of DOM. Hood et al. (2005) attributed a seasonal increase in SUVA values to a spring flush of labile DOC from accumulated microbial activity under snow pack in Colorado forested subalpine streams. In Arkansas, Brisco and Ziegler (2004) found the opposite seasonal trend in an undisturbed headwater stream that they attributed to increased algal growth during summer and photochemical breakdown of allochthonous DOC. In the current study, we suggest that a high degree of labile DOC input flushed during spring lead to a relative reduction in labile DOC during low flow sampling after depletion of the source. Autochthonous production was limited in our control streams due to high shade and so the importance of this pathway and photochemical reactions were limited. Old and new clearcut streams appeared to function differently from each other and from control streams throughout the season. New clearcuts tended to show a positive response in $SUVA_{350}$ during both sampling periods. Old clearcut streams were the only treatment where DOC seasonally shifted to a more labile pool indicated by decreased $SUVA_{350}$ effect between high and low flow. Next, we will discuss reasons for this differing response among treatments.

Treatment x Seasonal Response

Increased light and nutrient availability are two known responses to clearcut logging in the initial years following harvest. We suggest these factors acted together resulting in an opposite seasonal shift in old clearcuts, and alternate functioning within new clearcuts. Humic derived DOC exposed to light generally enhances the labile pool of DOC through photolysis (Tranvik and Bertilsson 2001; Brisco and Ziegler 2004). Increased heterotrophic activity follows photolysis by providing bioavailable DOC unless a further limiting factor exists. An initial nutrient flush followed by nutrient limitation is associated with removal of riparian vegetation (Gregory et al. 1987). An investigation of ESSF wc forest soils in close proximity to our study locations revealed that forest soil nitrogen concentrations more than doubled in the first year following clearcut logging, and then declined 4-5 years post harvest to less than reference conditions (Feller 1997; Hannam and Prescott 2003). In old clearcut streams, exposure to light during the summer may have broken down photoreactive compounds and lead to increased labile compounds. However, in combination with decreased nutrient availability, the labile pool of DOC likely accumulated throughout the summer due to reduced consumption by heterotrophic microbes compared with control streams.

Increased nutrient availability within new clearcuts provided a different scenario that lead to a decreased portion of refractory DOC. Ziegler and Brisco (2004) showed that elevated nutrients in a disturbed headwater stream supported more microbes and resulted in a larger pool of refractory DOC than a comparable forested stream. The authors reasoned that two processes lead to this result: microbial degradation of terrestrial organic matter released humic substances (generally aromatic carbons), and elevated microbial uptake of labile DOC increased the portion of refractory compounds. In the

present study, the refractory portion of DOC was elevated in new clearcuts in both seasons sampled, but particularly during low flow. DOC concentration tended to decrease seasonally more in new clearcuts than in control and old clearcut streams (Fig. 11a). Seasonal effects in new clearcuts differed from old clearcuts but not from control streams (Fig. 11b). Thus, we suggest that increased nutrients in new clearcuts, likely acting synergistically with photolytic production of labile DOC compounds, supported increased microbial activity throughout the summer. Although we did not examine microbial biomass, we suggest that microbial uptake of the labile pool would lead to the seasonal increase in the refractory pool of DOC compounds in new clearcuts. Heavily shaded control streams lacked the further addition of labile DOC through photolysis, but also lacked the additional consumption of labile DOC through elevated microbial biomass. Thus, the net effect of new clearcuts on aromaticity of DOC appeared similar to control streams.

Although canopy closure was similar between clearcut groups, and vegetation had not yet established significantly in either group, our results showed different temporal responses to forest harvesting. Generally, three main silviculture activities were completed following winter logging in our locations. In the initial year following logging we found that slash remained on most sites. Debris was generally burned and site preparation such as mounding occurred to expose mineral soil for tree planting the next summer. These silviculture activities take place within the time frame of our new clearcut treatment, and can take place immediately adjacent to S5 and S6 streams, which do not require a riparian reserve or machine free zone. Organic debris generally causes negative effects such as increased suspended sediment, although it is noted to mediate

temperature increases associated with logging (Jackson et al. 2001). We suggest that in new clearcuts organic debris caused elevated levels of FPOM and DOC and supplied photoreactive DOC compounds that in turn produced labile DOC when exposed to light. Organic debris would also supply increased nutrient availability to allow elevated biomass of stream heterotrophic biota that in turn depleted the supply of labile DOC (Fig. 12). This response may trigger a bottom up response in the stream food web if consumers of the heterotrophs are limited either by nutrient availability or by their prey.

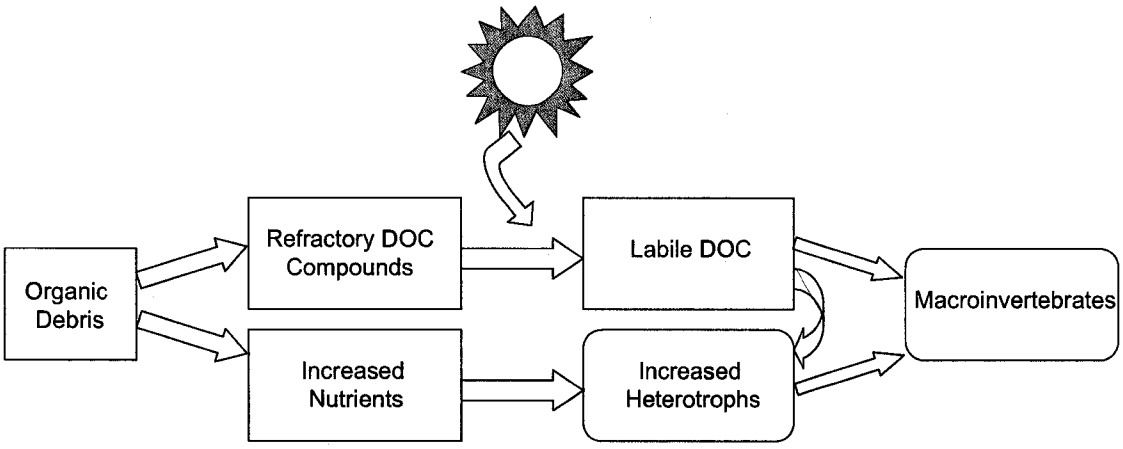

Figure 12. Schematic diagram showing the flow of energy from allochthonous sources and light to heterotrophs and macroinvertebrates.

An alternative or additional explanation to the changes in DOC is a photochemical pathway reported for autochthonous compounds. Algal derived compounds can condense on exposure to light thereby reducing the labile pool of DOC (Tranvik and Bertlisson 2001; Brisco and Ziegler 2004). This would also explain seasonal increased $SUVA_{350}$ in new clearcut streams if a smaller but important portion of DOC was derived from algae. We did not measure the influence of stream temperature, a factor shown to positively affect microbial production in headwater streams (Peters et al. 1987). In order to confirm or refute these pathways, a more complete dataset would be required such as measurements of nutrient levels, UVR penetration, and microbial

activity in clearcut streams. Analytical methods such as stable isotope analysis and fluorescence index analysis would assist in a further examination of the relative influences of algal, deciduous or coniferous vegetation on DOC.

Experimental Approach

There were several assumptions made in the design of this experiment. Hydrologic data for the headwater streams in this study do not exist and our discharge measurements were point data collected during high flow sampling only. Discharge is an important parameter that influences total export of organic matter in response to clearcut harvesting. In North Carolina, increased particulate organic matter (POM) standing crop occurred in small streams 16 and 30 years after clearcut harvesting (Silsbee and Larson 1983; Stone and Wallace 1998). Several authors have suggested that recovery from disturbance in northern streams may take longer than for temperate streams at lower latitude due to hydrology (Moore and Wondzell 2005), and differences in temperature regime (Macdonald et al. 2003b). In similar forest types to our study, increased discharge persists for at least 15 years in the montane spruce in the southern interior of BC (Winkler et al. 2005) and 30 years in the ESSF in Colorado (Troendle and King 1985). This response may cause increased annual export of organic matter even if concentrations do not differ among treatments. However, even intensive sampling of organic matter concentrations combined with hydrologic data underestimates export due to under representation of storms where most of POM transport occurs (Cuffney and Wallace 1988; Webster et al. 1990). Continuous hydrologic data in our treatments streams would have enabled the determination of minimum annual export rates.

We assumed a high degree of natural variability existed among our streams, making it difficult to use the reference stream approach. To address this issue we used mean differences between paired sites on control streams as a reference for the base condition. These differences were not always equal to zero, most notably there was a slight increase in DOC concentration within control streams from upstream to downstream during low flow, accompanied by a shift to more labile carbon composition of DOC. During high flow smaller differences in the same directions (+/-) occurred within control streams. It is expected that DOC concentrations increase longitudinally from the headwaters downstream, with cumulative inputs from detritus, and through contact with the upper soil horizon. Another factor during high flow sampling is diel fluctuations in DOC. We sampled downstream sites between 8 am and noon, and upstream sites between noon and 4 pm, to maintain consistency across treatments. These are two considerations that may account for differences in organic matter between paired sites on reference streams. Sampling bias was constant among treatments because we compared differences between two sites per stream, with similar physical attributes among all streams.

Summary

We found that FPOM transport increased initially in response to clearcutting, but recovered with 5 years. DOM transport did not change in response to clearcutting, but seasonally dependent composition of DOM was altered in clearcuts, and did not recover to pre harvest conditions within 7 years post harvest. Our results indicate that pathways of DOC utilization were altered in clearcuts. This was only evident during the low flow sampling period. The responses seen in this study were not necessarily detrimental to

stream biota, but could lead to a shift in community composition among trophic levels. The research has applicability to the ESSF forest, which has lacked investigation in the interior of the Pacific Northwest Region to date. It is a first step to quantify levels of organic matter transported in small streams, and to identify responses to forestry disturbance up to eight years post harvest. Future research should investigate whether responses occur in the longer term. Further investigation is warranted to determine if the responses we found translate to changes in annual export of organic matter and if stream biota respond to the alterations we reported.

Chapter 2: Effects of clearcutting on invertebrate drift within headwater streams in British Columbia, during two periods post harvest.

Abstract

Invertebrate drift exported from headwater streams subsidizes downstream food webs and alterations to invertebrate drift can affect fish production. We investigated effects of clearcut logging on density and composition of drift in headwater streams within Englemann spruce – subalpine fir (ESSF) forests in British Columbia in three treatment groups: "new" 1-3 years post harvest, "old" 5-7 years post harvest, and reference streams (non harvested). We compared mean differences between paired sites on streams for 52 biotic metrics. We used logistic regression and multiple linear regressions for common taxa to determine if disturbance predicted their presence/absence, and if fine particulate organic matter (FPOM) and dissolved organic carbon (DOC) predicted their densities. Seventeen of the 52 biotic metrics differed among treatments. Total invertebrate densities (abundance and biomass) increased due to clearcutting, but showed no signs of recovery as new and old clearcuts differed significantly from reference streams. Both aquatic and terrestrial invertebrate drift increased in steams flowing through clearcuts. Taxa within the orders Ephemeroptera and Diptera drove the increased drift. Scrapers increased in old clearcuts, whereas collector-gatherers contributed to response in both clearcut groups. Percent shredders responded negatively to both clearcut groups, and taxa richness weighted for abundance in each sample responded negatively to new clearcuts. Site location (upstream of or within clearcut) did not predict presence/absence of common families and genera, but FPOM concentration was positively related to density of family Chloroperlidae and the genus *Ameletus*. Our results indicate that

clearcut logging increased quantity and altered composition of invertebrate drift up to 7 years post harvest. We suggest that the response was primarily due to increased densities of the invertebrate benthic standing stock in clearcut streams. Changes in composition were likely due to increased benthic production that favoured multivoltine taxa, taxa that directly or indirectly benefited from increased primary production, and taxa that tend to drift. Implications for fisheries management are that short-term gains may occur, but long term stability in resources exported from headwater streams are uncertain.

Introduction

Due to the "fish-centric" nature of riparian forest management, small streams that are non-fish bearing are often the least protected in terms of a no harvest riparian buffer (Young 2000; Cummins and Wilzbach 2005). Fish such as salmonids, however, are seasonally food limited and may receive an important subsidy of organic matter from headwater reaches, especially when considering cumulative export (Wipfli and Gregovich 2002). It is important to consider cumulative impact because small streams exist in the highest numbers among the continuum of freshwaters and have the closest link between terrestrial and aquatic ecosystems (Vannote et al. 1980). Headwater streams are generally detrital based food webs that rely on a net import of allochthonous organic matter derived from the terrestrial ecosystem. A high degree of canopy closure results in relatively low primary production and cool water temperatures. Small streams have an important element of large woody debris that allows retention of suspended particles and also mediates discharge. The result of these characteristics is that headwater streams export a unique component of organic matter, including invertebrate drift, to subsidize downstream trophic webs.

Invertebrates enter the drift passively due to disturbance that causes habitat deterioration, for example increased suspended particles (Culp and Davies 1983), and actively for reasons that include predator avoidance, response to resource depletion, or as part of their life cycle (Brittain and Eikeland 1988). Water temperatures are closely linked to life cycle cues and can affect invertebrate drift through altering emergence times (Vannote and Sweeney 1980). Drift is density dependent, reported by Waters (1965) to be the subset of the benthos that exceeds its carrying capacity. Thus, increased

invertebrate production would lead to increased drift rates. Reduced habitat quality can stimulate invertebrates to enter the drift both actively (Kohler 1984) and passively (Culp and Davies 1983). Resource depletion likely stimulates increased drift and can cause short-term spikes in drift rates (Siler et al. 2001). Drift is positively correlated with, and has shown the same trends as, benthic assemblages in response to disturbance (Waters 1965; Siler et al. 2001). However, in response to food depletion or altered habitat quality, drift rates may increase and cause a decline in benthic densities (Brittain and Eikeland 1988).

Research on the effects of streamside clearcutting on invertebrate drift is lacking in comparison to the effects on invertebrate benthic densities. Yet, drift may be more closely related to fish production than benthos because a wide range of fish species subsist primarily on invertebrate drift (Hynes 1970). Although a small percentage of the benthic community (<1 %) is suspended in the drift at one time, daily drift rates over an area are much greater than the benthic standing crop of that area (Giller and Malmqvist 1998). Wipfli and Gregovich (2002) reported that export of drift and detritus can support 100-2000 young-of-the-year salmonids per kilometre of a fish bearing reach that receives water from headwater streams. In addition to the quantity of invertebrates drifting, the type of invertebrates in the drift may also influence fish resources. Terrestrial invertebrates that drop in from adjacent vegetation are known to be an important resource to drift feeding fish due primarily to their larger size, and make up 40-70 % of salmonid diet in summer months (Nakano et al. 1999; Kawaguchi and Nakano 2001). However, most animals require the low carbon:nitrogen ratio that autochthonous sources and certain species of deciduous riparian vegetation provide (Murphy and Meehan 1991).

Therefore, a shift from dominant allochthonous to autochthonous production may provide a higher quality food source for invertebrates and fish, if biota were facultative in their food sources. If logging affects the density or composition of invertebrates in the drift of headwater reaches, the response can carry through to affect fish production (Bilby and Bisson 1992; Hetrick et al. 1998). Since drift is a subset of the benthic community, effects of clearcut logging on benthic invertebrates are useful as comparisons to the effects on drift; however, the mechanism of the effect and characteristics of drift require consideration.

The main effects of streamside forest harvesting on small streams include decreased shade leading to elevated water temperatures (Brown and Krygier 1970) and increased primary productivity (Webster et al. 1983). In the initial years following logging, nutrient concentrations increase (Gregory et al. 1987) and allochthonous inputs decline (Bilby and Bisson 1992). Longer-term effects include increased water yields (Troendle and King 1985; Chamberlin et al. 1991), increased suspended particles (Macdonald et al. 2003a), and altered stream morphology due to a decline in large woody debris recruitment (Hicks et al. 1991). Increased light and increased autochthonous resources generally lead to increased benthic macroinvertebrate densities following clearcutting. For example, invertebrate densities increased three to five years following clearcutting in hardwood forests (Noel et al. 1986; Silsbee and Larson 1983; Stone and Wallace 1998). Studies in the Pacific Northwest reported increased benthic invertebrate densities in clearcuts within five years post harvest (Newbold et al. 1980; Fuchs et al. 2003; Kiffney et al. 2003; Hernandez et al. 2005). Conversely, Culp and Davies (1983)

found decreased benthic invertebrate densities, and increased drift rates in a coastal system within three years post harvest.

While macroinvertebrate assemblages generally increase following clearcutting, changes to community composition are more difficult to interpret. One method of tracking community changes is by categorizing organisms based on their food source and method of obtaining it. Taxa are categorized among five functional feeding groups: predators, collector-gatherers, collector-filterers, scrapers and shredders (Merritt and Cummins 1996). Two of these groups, scrapers and shredders, rely on the two main energy resources directly affected by forest harvest; light and organic matter. In headwater streams scrapers subsist primarily on aufwuchs, made up primarily of algae, and are influenced by increased light, and shredders consume leaf litter (Merritt and Cummins 1996). Collector-gatherers and collector-filterers subside on fine particles that are products of detritus, algae, and metabolic wastes. Therefore, collectors are affected by a shift in food base that may occur through increased primary production in the short-term, and increased detrital processing rates due to composition of early successional vegetation. Predators subsist on all non-predator groups and, therefore, the same factors that influence the remaining functional feeding groups indirectly affect predators (Hawkins et al. 1982). When invertebrate densities increased in response to clearcutting, scraper and collector-gatherer densities drove the response in the first 2-5 years post harvest (Webster et al. 1983; Gurtz and Wallace 1984; Hernandez et al. 2005), and shredder densities drove increased invertebrate densities in the longer term, 16 years (Stone and Wallace 1998) and 35-45 years post harvest (Hernandez et al. 2005). The

factors controlling the time frame in which scrapers decline and shredders begin to increase remains unclear.

Biotic metrics are also useful measures to track changes in composition and diversity. For example, densities of groups such as orders, families and functional feeding groups, taxa richness, indices of taxa heterogeneity and evenness, and consideration of organisms' reported tolerances to disturbance can be useful biotic metrics. Benthic bioassessment protocols commonly use many of these biotic metrics to assess stream health by comparing similarities between disturbed streams and reference conditions (Barbour et al. 1999). Alternatively, a multimetric approach evaluates a set of biotic metrics measured in streams along a gradient of disturbance to assess stream health relative to the degree of disturbance (Karr and Chu 1999). Biotic metrics are not commonly used to describe invertebrate drift as drift does not represent the entire macroinvertebrate community and, therefore, cannot directly represent stream health. However, we used biotic metrics to detect relative differences in drift densities and composition.

Among investigations of the effects of forestry in the Pacific Northwest Region, most research to date has focussed on southern and coastal areas. Some exceptions include findings in sub-boreal spruce forests in north central British Columbia. Fuchs et al. (2003) reported increased benthic densities, and Macdonald et al. (2003a, 2003b) reported increased temperature and suspended sediment in headwater streams. In montane spruce forest in the southern interior of B.C., Winkler et al. (2005) reported hydrologic effects of logging. In Englemann spruce subalpine fir (ESSF) forests, Heise (2001) reported altered benthic invertebrate functional feeding group representation and

decreased diversity up to five years post harvest in some but not all study streams. The ESSF biogeoclimatic zone covers 12 % of the province and is the highest elevation forested zone in the southern and central interior of British Columbia (DeLong and Meidinger 2003). Englemann spruce (*Picea englemanni)* is one of the most important commercial species in the interior due to its wood characteristics, and excellent source of pulp (Parish et al. 1996). Small streams and their responses to clearcut logging in ESSF forests have been studied very modestly considering their ecological and economic importance.

Our goal was to investigate invertebrate drift to determine if clearcut logging adjacent to headwater streams altered the export of prey to downstream fish bearing reaches. We also tested the hypothesis that, after any initial responses, invertebrate drift would recover within the first decade post harvest. We selected this time frame for several reasons. First, the Province of British Columbia implemented the Forest Practices Code in 1995 and in order to compare streams managed under the same umbrella of regulations, we selected streams harvested after 1995. Second, we selected a range of years with varying reports of response and recovery in headwater streams. Increased nutrients coupled with increased light cause elevated primary and secondary production within the first several years following harvest (Murphy and Meehan 1991), but it becomes unclear if recovery of the invertebrate community may occur in subsequent years within the first decade following harvest. Third, we investigated a relatively narrow range of years within each clearcut group to minimize variability within treatments. Therefore, we compared undisturbed ("control") streams in old growth ESSF forest to streams in "new clearcuts" 1-3 years post harvest, and streams in "old clearcuts"

5-7 years post harvest. We posed three questions with respect to our comparisons among "control", "old clearcuts" and "new clearcuts". First, we evaluated response of overall invertebrate drift to clearcutting during high seasonal discharge. Second, we investigated responses of the drift composition by utilizing a range of biotic metrics at varying taxonomic levels, and presence/absence of common families and genera. Third, we investigated whether fine particulate organic matter (FPOM) and dissolved organic carbon (DOC) levels were associated with drift rates of the common taxa that we identified.

Methods

Study Location

We conducted a comparative survey using paired sites located on each selected stream within the ESSF biogeoclimatic zone in the southern interior of British Columbia. Our requirements for selected watersheds within this forest type were that each stream be small, non-fish bearing and within clearcuts ranging from one to ten years post harvest for the treatment streams. Similar streams within undisturbed forest served as control streams. We also chose to examine two subzones within the ESSF biogeoclimatic zone. Of five candidate study areas identified in conjunction with tenure holders in the region, field reconnaissance determined that two of these areas, Bone Creek and Damfino Creek, met the criteria.

In 2004, we sampled twenty-two streams within Bone Creek and Damfino Creek (Fig. 13). Ten of the streams were within the Bone Creek study area, located approximately 255 km northeast of Kamloops and situated in the ESSF wet cold subzone Thompson Plateau variant (ESSF wc2; Lloyd et al. 1990). The ESSF wc2 is

characterized by 361 mm mean precipitation during the growing season, 782 cm mean annual snowfall, and 1.1 °C mean annual temperature. Bone Creek is a tributary of the North Thompson River, which supports numerous salmonid species. A waterfall is located 150 metres upstream from the mouth of Bone Creek that prevents fish passage, leaving the remainder of the watershed absent of fish (FRBC 2001).

The remaining twelve streams were within the Damfino Creek study area located approximately 260 km southeast of Kamloops within the ESSF dry cold subzone, Okanagan Highlands variant (ESSF dc1; Lloyd et al. 1990). The ESSF dc1 is characterized by 261 mm growing season precipitation; 635 cm mean annual snowfall and 2.0 ° C mean annual temperature (Lloyd et al. 1990). Sites in this study area were sampled within two watersheds: Damfino Creek and Two John Creek. Two John Creek is located ten kilometres south of Damfino Creek within the same biogeoclimatic zone and variant. A waterfall located 561 m from the mouth of Damfino Creek prevents fish passage to the upstream reaches, and barriers restrict fish migration in the upper reaches of Two John Creek where sample streams were located (FRBC 2000). Damfino Creek flows into the Kettle River, and Two John Creek flows into the West Kettle River, which then flows into the Kettle River. The Kettle River is a tributary of the Columbia River and supports numerous salmonid species.

All streams selected in this study fall under the S6 stream classification, which includes non fish bearing streams no greater than 3 m bank-full width under British Columbia's Forest and Range Practices Act. Cutblocks selected in this study ranged in size from 20 to 95 ha and contained up to 24 identified S6 streams within one block. Best management practices prescribed retention of the most windfirm 5 % of codominant

conifers within 20 m of the channels of two streams for every 40 ha of harvest area, and full retention of non-merchantable vegetation within 5 m (Province of BC 1995). All treatment streams were nearly to completely void of conifers in their riparian zones, and where conifers remained they were early seral and sparse. A portion of streams in each treatment had non-merchantable vegetation left in the riparian zone that comprised deciduous species such as alder (*Alnus tenufolia)* and rhododendron (*Rhododendron albiflorum)*. The primary logging method used within the Damfino study area streams was conventional grapple skidding, while high lead yarding was common in the Bone Creek study area due to steeper topography.

Although this study was not designed to quantify or evaluate the effects of slash, organic matter left in or adjacent to streams is considered an important influence on stream responses to clearcut logging. Our observations were that slash presence was variable among clearcut streams ranging from very little slash present immediately adjacent to the channel, to high amounts of slash that covered the stream channel. The specific influence of slash was not tested in this study, as the objective was to evaluate effects of the end result from clearcut harvesting, regardless of site-specific differences in logging operations.

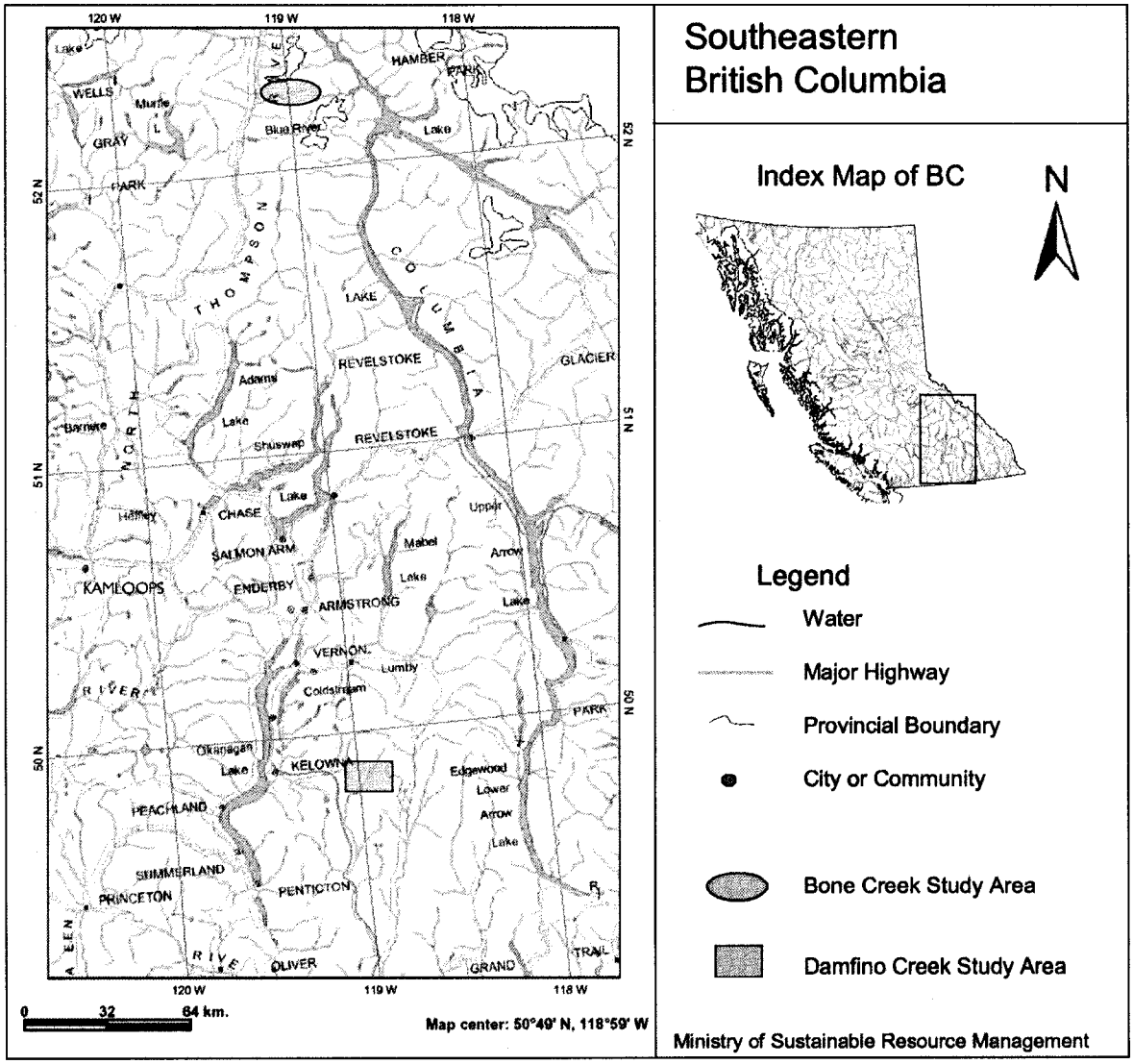

Figure 13. Locations of Bone Creek and Damfino Creek study areas within the southern interior of British Columbia.

Experimental Design

The selected streams fell into one of three treatment categories: "control" streams, "new" clearcuts (1-3 years post harvest), and "old" clearcuts (5-7 years post harvest). The minimum distance that a stream flowed through its associated cutblock was 300 metres at Bone Creek and 250 metres at Damfino Creek. Therefore, this minimum distance separated the downstream site from the upstream forest edge, and an additional

50 metres separated the forest edge from the upstream site (Fig. 14). The same distances separated control stream paired sites located at elevations and physical characteristics representative of treatment streams. Streams served as replicate sampling units to avoid issues of pseudoreplication (Hurlbert 1984).

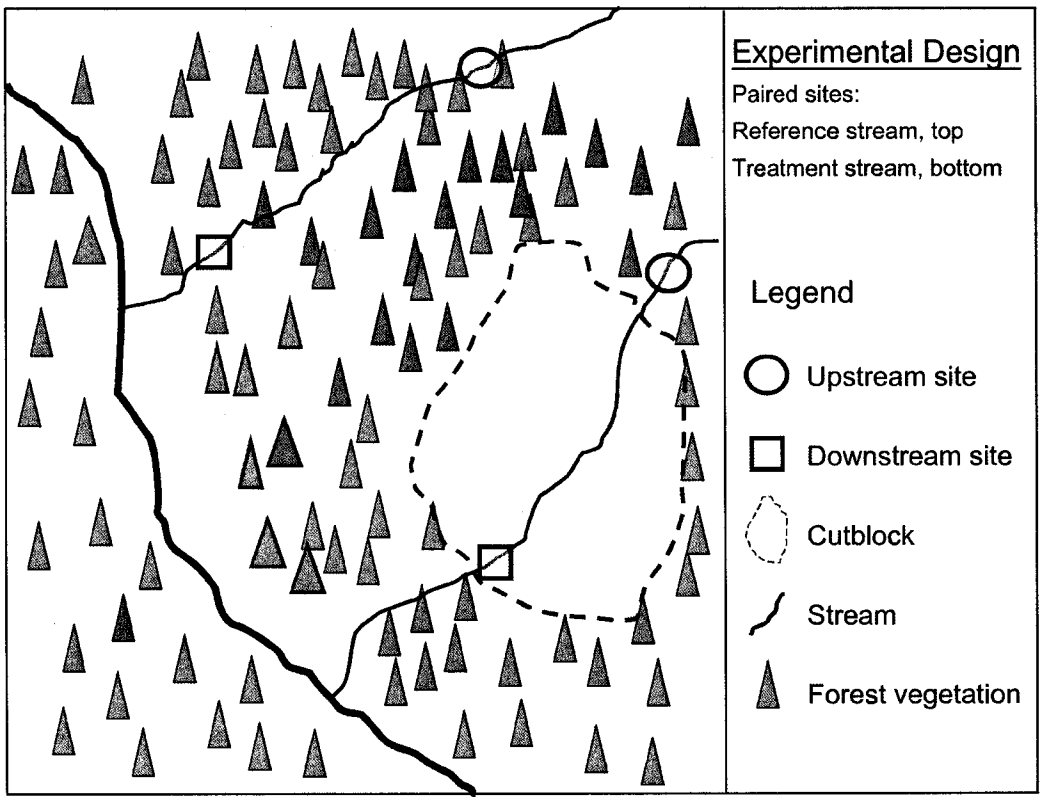

Figure 14. Schematic diagram illustrating the experimental design.

We addressed potentially confounding variables by judicious site selection and timing of sampling. We maintained a consistent slope distance between paired sites in order to reduce variability associated with effects that may occur as a function of reach length. We excluded streams if they had insufficient flow to use appropriate drift sampling methods (described below), if they flowed through a known disturbance upstream from the selected clearcut, and if they contained a riparian reserve zone, defined as an undisturbed area of timber adjacent to the stream. To avoid the additional influence

of roads, we excluded streams if they contained active or decommissioned roads larger than skid trails within the paired sites. We selected reference streams with a range of physical characteristics comparable to treatment streams.

Timing of sampling influences drift rates due to seasonal and diel periodicity, and discharge pulses. Due to the influence of hydrology on drift, we did not sample during or following heavy rainfall. We commenced sampling at the same time each day with downstream sites in the morning followed by upstream sites in the afternoon. We began sampling at the period of high flows and, therefore, maximum drift in order to maximize sampling efficiency. The onset of maximum flows at Bone Creek begins later than Damfino Creek due to its glacial source and higher latitude. Therefore, we began sampling at Bone Creek following completion of sampling at Damfino Creek. To avoid bias from seasonal fluctuations, we alternated the sampling among treatments at each study area, as opposed to sampling all control streams then all clearcut streams.

Data Collection

We recorded physical characteristics at each site including canopy closure, discharge, bank-full channel width, stream gradient, aspect and elevation (Table 3). At two locations for each site we used a densiometer held 1 m above ground facing four directions and averaged the readings to determine canopy closure (Lemmon 1956). We measured discharge by recording the time to fill a large container of known volume at least three times and obtaining the average (Gore 1996). Bank-full channel widths were measured at three locations and averaged; gradient and aspect were measured using a clinometer and compass. Elevation and UTM coordinates were taken by GPS at each site location and elevations were verified using topographical maps. Temperature loggers

were placed in streams at each site and temperature was recorded hourly over at least twenty-four hours. We collected dissolved organic carbon (DOC) and fine particulate organic matter (FPOM) samples preceding invertebrate drift sampling at each site, and at an additional sampling period during low flow. Methodologies for these variables and spectral ultraviolet absorbance ($SUVA_{350}$) are described in Chapter 1.

We sampled invertebrate drift in triplicate at each site using a drift net with collecting bucket and standard mesh size of 254 μm. Samples were stored in 70 % ethanol in Whirl-Pak® bags and later sorted and identified in the lab under 10-80x magnifications. Total body lengths of organisms were measured using an ocular micrometer and biomass was calculated using length-weight regressions from the literature (Smock 1980; Sample et al. 1993; Burgherr and Meyer 1997; Benke et al. 1999), or average dry mass per individual for taxa not represented in the literature (see Appendix 1). For these organisms, a sample of 20-30 individuals taken from numerous samples was dried at 60 °C for at least 24 hours, and average dry weight per individual was calculated as an estimation of biomass. All organisms were identified to family except the following taxonomic groups that were not further identified: Collembola, Isopoda, Branchiopoda, Cladocera, Copepoda, Ostracoda, Nematoda, Nematomorpha, Platyhelminthes, Oligochaeta. The orders Ephemeroptera, Plecoptera, Trichoptera (E,P,T; mayflies, stoneflies and caddisflies, respectively) were further identified to genus using Merritt and Cummins (1996), Stewart and Stark (2002), and Wiggins (1996).

Table 3. Physical characteristics and sampling dates of study streams sampled in 2004 within the Bone Creek and Damfino Creek study areas.

Stream ID [a]	Treat-ment	Year logged	Canopy closure (%) [b]	Discharge (L sec^{-1})	Bank-full width (m)	Stream gradient (%)	Aspect	Elevation median [c] (m)	Water Temp.[d] Min (° C)	Water Temp.[d] Max (° C)	Date Sampled (2004)
Bone Creek											
005	Control	-	25	5.46	0.47	35	W	1184	9.8	14.8	14-Aug
012	Control	-	78	12.38	2.72	34	E	1131	8.9	12.3	24-Aug
013	Control	-	94	2.39	2.13	32	SE	1297	5.7	7.6	19-Aug
025	Control	-	52	4.28	0.61	32	NE	1671	7.9	9.9	27-Aug
021	New	2003	0	1.31	0.85	41	S	1536	9.9	11.8	13-Aug
023	New	2003	0	0.59	0.68	31	S	1845	6.1	12.3	13-Aug
002	New	2002	42	0.63	0.94	57	E	1453	n.d.	n.d.	25-Aug
027	New	2001	59	3.42	1.03	65	SW	1543	8.8	9.2	29-Aug
010	Old	1999	0	0.43	2.50	58	N	1262	9.5	11.6	12-Aug
011	Old	1998	0	1.66	1.00	33	NE	1171	9.2	11.8	26-Aug
Damfino Creek											
203	Control	-	77	4.16	1.63	4	SW	1566	4.6	12.0	26-Jun
208	Control	-	5	4.29	0.71	18	S	1592	8.4	8.6	9-Jul
209	Control	-	73	4.11	1.56	23	NW	1820	6.5	16.0	11-Jul
213	Control	-	84	1.17	1.04	12	NE	1682	n.d.	n.d.	21-Jul
201	New	2003	63	19.04	0.86	7	SE	1547	5.5	12.0	18-Jun
205	New	2003	17	3.77	1.02	14	N	1660	7.3	11.2	29-Jun
207	New	2003	55	5.63	0.76	14	SE	1730	6.1	19.9	10-Jul
215	New	2003	57	1.47	1.62	16	NE	1652	n.d.	n.d.	23-Jul
206	Old	1998	92	1.41	1.01	9	E	1873	6.4	16.7	30-Jun
210	Old	1998	18	0.18	1.30	24	N	1825	7.4	10.0	13-Jul
211	Old	1998	39	0.92	0.76	27	W	1830	6.2	8.5	14-Jul
202	Old	1997	45	2.69	0.86	8	W	1695	n.d.	n.d.	25-Jun

Note: Attributes measured during high flow sampling period with multiple measurements at each site. Stream average values are presented with the exception of canopy closure, which are given for downstream sites for comparison of logged versus old growth.

[a] All streams are unnamed; therefore, each stream was assigned a number with the leading digit indicating study area

[b] Canopy closure represents percentage of cover measured by densiometer 1 m above ground at downstream sites

[c] Represents the median elevation between downstream and upstream paired sites

[d] Water temperaure logged hourly over at least 24 hours during sampling date of each stream

Data Analysis

Biotic Metrics

All organisms were categorized as aquatic or terrestrial and were assigned to the functional feeding groups of predators, collector-gatherers, collector-filterers, scrapers and shredders based on Merritt and Cummins (1996). Semi-voltine organisms were considered long-lived. Using a database prepared for the Pacific Northwest by Robert Wisseman and Leksa Fore (SalmonWeb 2001), taxa were assigned a Hilsenhoff tolerance value (Hilsenhoff 1982), and designations as intolerant to organic pollution and clinger taxa. Clinger taxa not listed in this source were classified according to Merritt and Cummins (1996). The Hilsenhoff Biotic Index (HBI) and intolerant designations are regionally specific and have not been tested for our study area, but have been used previously for bioassessment in the central interior of BC (Bennett and Hewgill 2002; Croft 2003). Terrestrial taxa and indistinct taxa were excluded from calculation of HBI. Indistinct taxa are defined as those not identified to the lowest levels previously stated due to immature or damaged specimens. Indistinct taxa were included in metrics that sum total invertebrates and in sums of orders and families depending on their level of identification. Diversity metrics included indistinct taxa if they were identified to the family level and no other family member was collected at that site. All taxa in Bone Creek and Damfino Creek drift samples and their designations are listed in Appendix 1.

We quantified the density of invertebrates by abundance and biomass of organisms per volume of water in each replicate for the following groups: total invertebrates, aquatic invertebrates, terrestrial invertebrates, Ephemeroptera, Plecoptera, Trichoptera, Diptera, sum of EPT, sum of EPT divided by D, and the five functional

feeding groups (Table 4a). Percentages of invertebrates categorized as aquatic, terrestrial, E,P,T,D, clinger, non-insect, long-lived, intolerant, and each functional feeding group were calculated as abundance of each group divided by abundance of total invertebrates, and the Hilsenhoff Biotic Index (HBI) was calculated for each replicate (Table 4b). We used additional biotic metrics defined by Karr and Chu (1999) and Krebs (1999) to detect responses in diversity of the drift community (Table 4c). There were 52 variables in total and we refer to the group as biotic metrics.

Table 4. Definitions of the 52 biotic metrics calculated based on the designations for each taxon (Appendix 1) identified from drift samples in Bone Creek and Damfino Creek. Biotic metrics are organized into three assessment categories: a) Densities, (b) Biotic indicators, and (c) Diversity.

a) Densities The following metrics each represent two variables: abundance divided by volume of water (# organisms m^{-3}), and biomass divided by volume of water (mg m^{-3}).
Invertebrate density: The average density of total invertebrates collected in the three samples at each site.
Aquatic Taxa density: The average density of aquatic taxa collected in the three samples at each site.
Terrestrial Taxa: The average density of terrestrial taxa collected in the three samples at each site.
Ephemeroptera density: The average density of Ephemeroptera (E) collected in the three samples at each site.
Plecoptera density: The average density of Plecoptera (P) collected in the three samples at each site.
Trichoptera density: The average density of Trichoptera (T) collected in the three samples at each site.
Diptera density: The average density of Diptera (D) collected in the three samples at each site.
EPT density: The average density of the sum of all Ephemeroptera, Plecoptera, and Trichoptera individuals collected in the three samples at each site. (Resh and Jackson 1993)
EPT/D abundance: The average density of the sum of all Ephemeroptera, Plecoptera, and Trichoptera divided by Diptera individuals collected in the three samples at each site. (Resh and Jackson 1993)
Predators: The average density of predators collected in the three samples at each site.
Collector-gatherers: The average density of collector-gatherers collected in the three samples at each site.
Collector-filterers: The average density of collector-filterers collected in the three samples at each site.
Scrapers: The average density of scrapers collected in the three samples at each site.
Shredders: The average density of shredders collected in the three samples at each site.

Table 4 (Continued).

b) Biotic indicators.
% Aquatic: The abundance of aquatic individuals divided by the total number of individuals in each sample, averaged among three samples per site.
% Terrestrial: The abundance of terrestrial individuals divided by the total number of individuals in each sample, averaged among three samples per site.
% Ephemeroptera: The abundance of Ephemeroptera divided by the total number of individuals in each sample, averaged among three samples per site. (Karr and Chu 1999)
% Plecoptera: The abundance of Plecoptera divided by the total number of individuals in each sample, averaged among three samples per site. (Karr and Chu 1999)
% Trichoptera: The abundance of Trichoptera divided by the total number of individuals in each sample, averaged among three samples per site. (Karr and Chu 1999)
% Diptera: The abundance of Diptera divided by the total number of individuals in each sample, averaged among three samples per site. (Karr and Chu 1999)
% Clingers: The abundance of clingers divided by the total number of individuals in each sample, averaged among three samples per site. (Karr and Chu 1999)
% Non-insects: The abundance of non-insect individuals divided by the total number of individuals in each sample, averaged among three samples per site. (Karr and Chu 1999)
% Long lived individuals: The abundance of long-lived individuals divided by the total number of individuals in each sample, averaged among three samples per site. (Karr and Chu 1999)
% Intolerant: The abundance of intolerant individuals divided by the total number of individuals in each sample, averaged among three samples per site. (Karr and Chu 1999)
% Predators: The abundance of predators divided by the total number of individuals in each sample, averaged among three samples per site. (Karr and Chu 1999)
% Collector-gatherer: The abundance of collector-gatherers divided by the total number of individuals in each sample, averaged among three samples per site. (Karr and Chu 1999)
% Collector-filterer: The abundance of collector-filterers divided by the total number of individuals in each sample, averaged among three samples per site. (Karr and Chu 1999)
% Scrapers: The abundance of scrapers divided by the total number of individuals in each sample, averaged among three samples per site. (Karr and Chu 1999)
% Shredders: The abundance of shredders divided by the total number of individuals in each sample, averaged among three samples per site. (Karr and Chu 1999)
Hilsenhoff Biotic Index (HBI): The sum of abundance weighted by assigned tolerance to organic pollution value for each taxon, averaged among three samples per site. (Hilsenhoff 1982).

Table 4 (Continued).

c) Diversity. Measures of diversity, evenness and heterogeneity among taxa in drift samples.

Total taxa richness: The total number of distinct taxa counted in the three samples at each site. Distinct taxa includes individuals identified only to family/order if there were no individuals identified to a lower level for that taxon (Resh and Jackson 1993, Karr and Chu 1999).

Total taxa diversity density: Cumulative number of distinct taxa in three samples at each site divided by total number individuals counted in the three samples. (Karr and Chu 1999, Krebs 1999).

Ephemeroptera taxa diversity density: Cumulative number of distinct Ephemeroptera taxa in three samples at each site divided by total number individuals counted in the three samples. (Karr and Chu 1999, Krebs 1999).

Plecoptera taxa diversity density: Cumulative number of distinct Plecoptera taxa in three samples at each site divided by total number individuals counted in the three samples. (Karr and Chu 1999, Krebs 1999).

Trichoptera taxa diversity density: Cumulative number of distinct Trichoptera taxa in three samples at each site divided by total number individuals counted in the three samples. (Karr and Chu 1999, Krebs 1999).

Clinger taxa diversity density: Cumulative number of distinct clinger taxa in three samples at each site divided by total number individuals counted in the three samples. (Karr and Chu 1999, Krebs 1999).

Reciprocal of Simpson's index: Describes heterogeneity using cumulative numbers of taxa in three replicates at each site. The index was calculated using Ecological Methodology software (Krebs 1999).

$$1/D = \frac{1}{\sum P_i^2}$$

1/D = reciprocal of Simpson's index
P_i = Proportion of species *i* in the community

Smith and Wilson's index of evenness: Describes evenness of the distribution among taxa based on variance in abundance of each taxon. This index was calculated using cumulative numbers of taxa in three replicates at each site. (Krebs 1999). The index was calculated using Ecological Methodology software (Krebs 1999).

$$E_{var} = 1 - \left[\frac{2}{\pi \arctan\left\{ \sum_{i=1}^{s} \left(\log_e(n_i) - \sum_{j=1}^{s} \log_e(n_j)/s \right)^2 \div s \right\}} \right]$$

E_{var} = Smith and Wilson's index of evenness
n_i = Number of individuals in taxon *i* in sample
n_j = Number of individuals in taxon *j* in sample
s = Number of taxa in entire sample.

For each biotic metric, we determined effect as the difference between paired sites weighted for the sum of the metric within each stream (Equation 3). Effect ranges from –100 % to +100 %, and the effect formula achieves equal effects whether there is a positive or negative difference between sites over the same order of magnitude. For example, if there was a near zero value (0.0001 individuals m^{-3}) at the upstream site, and a value of 0.5 individuals m^{-3} at the downstream site, effect approaches 100 %. In the opposite situation, with 0.5 individuals m^{-3} at the upstream site and nearly zero at the downstream site, effect approaches –100 %. A positive effect indicates the metric increased after flowing through the clearcut, and a negative effect indicates the metric decreased after flowing through the clearcut. Control stream effects served as the base condition to compare against treatment stream effects.

$$Effect = \left[\frac{ds - us}{ds + us}\right] \times 100 \qquad \textit{Equation 3}$$

Where *ds* = downstream site metric value and *us* = upstream site metric value.

All data were checked for normality and homoscedasticity. Where there were deviations among the data, transformations such as log (x+1), Ln (x+1), and arcsin (sqrt(x)) were applied both to the raw data prior to calculating effects, and to the effect variables (Zar 1984). The transformation, however, did not improve deviations from normality or homoscedasticity. Therefore, we continued biotic metric effect analysis on the basis that ANOVA is robust to minor deviations from these assumptions.

To assess the appropriateness of pooling data from the two study areas, we used a two-way ANOVA with treatment and study area as fixed factors. If there were no significant results for study area and no interactions between study area and treatment ($p>0.05$), we pooled the data and used single factor ANOVAs to detect differences

among treatments for the remaining variables with *a priori* contrasts. Contrasts were chosen to detect differences between the following groups: *i)* control and old clearcuts, *ii)* control and new clearcut streams, and *iii)* old and new clearcut streams. The method of comparing differences between sites spanning a disturbance using control streams as the base condition is effective for detection of responses to disturbance (Underwood 1994).

EPT Families and Genera

The effectiveness of the preceding analysis was reliant on summing organisms at a level that was common between study areas, and standardizing metrics for each stream using "effect". At lower taxonomic groups, it was inappropriate to use the same approach for two reasons. Many families and genera were unique to each area making it impossible to pool study areas. Additionally, three quarters of the taxa occurred in less than 20 % of the replicates. There were many empty cells at the family and genus levels and applying the effect formula would result in either zero change for these streams or 100 % if only one of the pair was zero. Therefore, presence/absence data were more appropriate for analysis of treatment responses.

We excluded families and genera that occurred as less than 1 % of total invertebrates on average in each study area. We selected all clearcut streams in Bone Creek (n=12) and Damfino Creek (n=16) and compared presence/absence data for each selected taxon as dependent variables in logistic regressions. Site location was entered as the categorical predictor variable with an indicator contrast that compared downstream to upstream as the reference condition (SPSS® Version 11.0, SPSS Inc., 2005). The minimum number of cases to independent variables recommended is 10 and there are no

assumptions of normality, linearity or homoscedasticity in logistic regression (Hosmer and Lemeshow 2000).

In the preceding chapter, we reported that FPOM increased in response to new clearcuts, and DOC responded between high and low flow sampling periods in old clearcuts. To investigate whether these effects transferred to stream biota, we used multiple linear regression analyses to assess the ability of FPOM, DOC and $SUVA_{350}$ to predict abundance of common taxa. We conducted this analysis on lowest taxonomic levels because differing requirements among taxa of higher levels tend to mask specific responses to disturbance (Karr and Chu 1999). To reduce number of variables and to address correlations between variables, we first subjected DOC, $SUVA_{350}$, and FPOM to principal components analysis (PCA) using SPSS® (Version 11.0, SPSS Inc. 2005). Suitability of the data for PCA was assessed with the following results (Tabachnick and Fidell 1989). Cases included all sites (n=44) resulting in a ratio of cases to variables of 14 that exceeded the minimum recommendation of five. Several coefficients greater than 0.3 occurred in the correlation matrix indicating suitable correlations among variables. The Kaiser-Meyer-Oklin value was 0.519, and measures of sampling adequacy exceeded 0.500 for each variable. Bartlett's Test of Sphericity was significant ($p<0.001$). We extracted two components with eigenvalues greater than 0.9 based on examination of the scree plot. The components individually explained 59.5 % and 31.5 % of the variance for a cumulative 91 % of the variance. We used oblimin rotation to improve interpretability and the rotated solution indicated a simple structure with DOC and SUVA loading highly on the first component, and FPOM highly on the second (Table 5). DOC and SUVA are

closely related as raw variables, and their linear combination into a component allowed their use with FPOM as independent variables in multiple linear regressions.

Table 5. Structure matrix of the two factor solution for organic matter variables. Oblimin rotation with Kaiser normalization was used.

Variable	Component 1 DOC	Component 2 FPOM
DOC	0.92	
SUVA	0.90	
FPOM		0.93
% of Variance explained	59.50%	31.40%

Note: Only loadings above 0.4 are displayed

Results

Biotic Metrics

We identified 78 distinct taxonomic groups within 11 classes and within 11 orders of insects in drift samples from Bone and Damfino Creek study areas (Appendix 1). Diptera made up 38 % of invertebrate abundance in drift samples on average, the majority of these being Chironomidae larvae (14 %) and Diptera adults (13 %). Collembola made up 16 %, Plecoptera 12 %, Arachnida 9 %, Ephemeroptera 7 %, Crustacea 5 %, and the remaining orders of insects and phyla of worms made up less than 5 % of the drift samples.

Mean total invertebrate drift density was 22 individuals m^{-3} (SEM=3 m^{-3}, n=44), and mean biomass was 5.10 mg m^{-3} (SEM=0.95 mg m^{-3}, n=44) among all sites in both study areas. Tables 6 and 7 summarize the means of biotic metrics among treatments in each study area.

Table 6. Mean biotic metrics (SEM) for downstream sites at Bone and Damfino Creek study areas among treatments. Category A biotic metrics are summarized.

	Bone Creek			Damfino Creek		
Biotic Metric	**Control**	**Old**	**New**	**Control**	**Old**	**New**
Abundance [a]						
Total Invertebrates	23 (9)	23 (4)	34 (12)	10 (4)	23 (8)	18 (4)
Aqu. Invertebrates	15.0 (4.0)	20.1 (3.9)	29.0 (9.5)	5.7 (1.6)	13.4 (3.8)	11.2 (2.7)
Terr. Invertebrates	7.8 (6.1)	3.2 (0.3)	4.4 (2.8)	4.4 (2.5)	9.9 (5.9)	7.1 (2.2)
Ephemeroptera	2.4 (1.1)	6.7 (1.1)	1.8 (0.8)	0.8 (0.1)	0.8 (0.4)	0.5 (0.2)
Plecoptera	2.0 (0.7)	1.4 (0.8)	1.6 (0.4)	1.1 (0.3)	1.8 (0.9)	2.8 (1.7)
Trichoptera	0.6 (0.1)	2.3 (1.2)	2.0 (0.6)	0.3 (0.2)	0.3 (0.2)	0.2 (0.1)
Diptera	6.8 (3.6)	9.4 (1.9)	22.6 (12.2)	4.2 (2.5)	10.3 (3.3)	8.1 (1.8)
EPT	5.0 (1.7)	10.4 (3.1)	5.1 (1.6)	2.1 (0.5)	2.8 (1.0)	3.6 (1.7)
EPT/D (no units)	1.1 (0.4)	1.1 (0.01)	0.5 (0.2)	1.4 (0.7)	0.3 (0.1)	0.9 (0.4)
Predators	3.3 (0.8)	4.0 (0.6)	11.0 (5.5)	2.5 (0.9)	5.1 (1.7)	3.5 (0.1)
Collector-gatherers	5.9 (1.5)	10.8 (2.0)	12.9 (4.2)	1.4 (0.5)	3.4 (1.6)	2.6 (0.9)
Collector-filterers	0.9 (0.8)	0.2 (0.2)	0.3 (0.1)	0.9 (0.7)	2.4 (1.7)	1.4 (0.6)
Scrapers	0.3 (0.1)	1.3 (0.4)	0.6 (0.3)	0.07 (0.05)	0.08 (0.08)	0.05 (0.03)
Shredders	1.9 (0.7)	1.6 (1.0)	1.9 (0.5)	0.3 (0.1)	0.8 (0.6)	2.2 (1.8)
Biomass [b]						
Total Invertebrates	1.8 (0.69)	12.5 (11.2)	9.8 (5.8)	2.2 (0.8)	11.7 (5.9)	5.9 (1.1)
Aqu. Invertebrates	1.3 (0.5)	1.1 (0.2)	8.9 (6.0)	1.3 (0.5)	6.7 (1.9)	2.8 (1.4)
Terr. Invertebrates	0.5 (0.2)	11.4 (11.0)	0.8 (0.5)	0.9 (0.4)	8.1 (6.3)	3.1 (1.4)
Ephemeroptera	0.4 (0.2)	0.2 (0.04)	0.4 (0.4)	0.2 (0.1)	0.1 (0.1)	0.3 (0.3) $\mu g\ m^{-3}$
Plecoptera	0.14 (0.04)	0.10 (0.09)	0.16 (0.09)	0.10 (0.02)	0.27 (0.17)	1.19 (1.12)
Trichoptera	0.39 (0.32)	0.13 (0.03)	7.04 (5.57)	0.36 (0.20)	0.93 (0.75)	0.92 (0.52)
Diptera	0.15 (0.07)	0.47 (0.15)	0.99 (0.49)	0.32 (0.15)	0.94 (0.36)	0.48 (0.21)
EPT	0.96 (0.45)	0.47 (0.09)	7.64 (6.02)	0.62 (0.29)	1.34 (0.71)	2.12 (1.44)
EPT/D (no units)	8.3 (3.6)	1.6 (0.2)	11.6 (5.8)	2.0 (0.9)	1.6 (0.7)	0.4 (0.4)
Predators	0.13 (0.06)	0.21 (0.06)	0.61 (0.25)	0.49 (0.23)	1.55 (0.93)	0.23 (0.16)
Collector-gatherers	0.48 (0.19)	0.44 (0.02)	2.40 (1.73)	0.27 (0.13)	0.59 (0.26)	0.21 (0.13)
Collector-filterers	0.03 (0.02)	1 (1) $\mu g\ m^{-3}$	1.02 (0.83)	0.17 (0.14)	0.39 (0.31)	0.16 (0.05)
Scrapers	0.09 (0.06)	0.11 (0.03)	0.30 (0.22)	0.03 (0.02)	0.1 (0.1)	8 (8) $\mu g\ m^{-3}$
Shredders	0.35 (0.23)	0.16 (0.15)	4.43 (4.30)	0.10 (0.04)	0.95 (0.67)	1.6 (1.5)

Note: There are 4 streams in each treatment except Bone Creek old clearcuts, n=2.

[a] Number of individuals m^{-3}; [b] mg m^{-3} except where noted.

Table 7. Mean biotic metrics (SEM) in downstream sites at Bone and Damfino Creek study areas among treatments. Category B metrics that are inherent from Table 6 are omitted, and all category C metrics are summarized. HBI = Hilsenhoff Biotic Index.

	Bone Creek			Damfino Creek		
Biotic Metric	**Control**	**Old**	**New**	**Control**	**Old**	**New**
% clingers	2.42 (0.66)	3.21 (2.13)	5.32 (1.45)	5.24 (4.17)	1.07 (0.85)	0.35 (0.31)
% non-insects	27.13 (9.78)	10.60 (4.25)	13.60 (5.35)	18.33 (3.52)	25.58 (6.48)	14.49 (5.05)
% long-lived	0.25 (0.13)	0.00 (0)	2.21 (1.03)	1.35 (0.64)	1.56 (0.92)	0.79 (0.67)
% intolerant	2.31 (0.85)	5.08 (2.91)	3.07 (1.03)	0.57 (0.35)	0.92 (0.67)	0.24 (0.14)
HBI	4.12 (0.68)	4.81 (0.02)	4.70 (0.18)	2.97 (0.44)	3.53 (0.38)	2.80 (0.80)
Taxa richness	25 (3)	17 (3)	21 (2)	18 (3)	17 (3)	17 (2)
Taxa div. density	0.10 (0.03)	0.25 (0.03)	0.16 (0.06)	0.24 (0.04)	0.30 (0.08)	0.21 (0.10)
E div. density	0.27 (0.16)	0.09 (0.02)	0.14 (0.09)	0.23 (0.02)	0.41 (0.22)	0.25 (0.25)
P div. density	0.12 (0.04)	0.47 (0.13)	0.43 (0.20)	0.21 (0.03)	0.56 (0.19)	0.28 (0.24)
T div. density	0.46 (0.10)	0.75 (0.25)	0.45 (0.11)	0.93 (0.11)	0.33 (0.24)	0.53 (0.27)
Clinger div. density	0.19 (0.05)	0.53 (0.07)	0.35 (0.11)	0.33 (0.05)	0.63 (0.22)	0.39 (0.21)
Heterogeneity [a]	6.30 (1.46)	4.86 (0.33)	4.91 (1.84)	6.58 (1.49)	5.45 (0.73)	4.92 (1.62)
Evenness [b]	0.34 (0.04)	0.52 (0.01)	0.45 (0.07)	0.52 (0.04)	0.61 (0.08)	0.45 (0.11)

Note: There are 4 streams in each treatment except Bone Creek old clearcuts, n=2.
Div. Density= Diversity Density, units in # taxa per individual.
[a] Reciprocal of Simpson's Index; [b] Smith and Wilson's Index of Evenness.

Biotic Metrics: Effect (%) Compared Among and Between Treatments

There were no significant interactions between treatment and study area ($p>0.05$), and study area did not significantly contribute ($p>0.05$) to the general linear model for a subset of the first fourteen biotic metric effect variables. This indicated that study area did not influence biotic metric effect variables and it was appropriate to pool data from the two study areas for further analysis.

Of the 52 response variables compared among and between treatments using single factor ANOVA and *a priori* contrasts, ANOVA detected significant differences among treatments for 11 metrics, and *a priori* contrasts detected differences between treatments in an additional six metrics. Table 8 presents the mean effects (%) among treatments for each of these variables, and gives p values for each test ($\alpha=0.05$). The 17 biotic metrics showed several different trends, and are presented in Table 8 according to

having a positive or negative response to both clearcut groups, new clearcuts or old clearcuts.

Table 8. Biotic metrics that differed for comparisons among (ANOVA) and between (contrasts) treatments of downstream-upstream effect in Bone and Damfino Creek study areas. Mean effect represents the difference between sites as a percentage.

Trend group	**Mean Effect (SEM)**			**ANOVA**	**Contrasts (p values)**		
Biotic Metric	**Control**	**Old**	**New**	**p value**	**Ctrl-New**	**Ctrl-Old**	**Old-New**
Positive response to clearcuts							
Total Invertebrates (Abd)	-34 (9)	15 (8)	27 (9)	0.000	0.000	0.002	0.338
Total Inverterbates (Biom)	-31 (10)	27 (25)	45 (13)	0.005	0.002	0.019	0.419
Aquatic Invertebrates (Abd)	-15 (7)	28 (9)	33 (11)	0.002	0.001	0.004	0.727
Diptera (Abd)	-30 (11)	21 (15)	43 (13)	0.002	0.001	0.016	0.259
Diptera (Biom)	-10 (18)	61 (16)	38 (14)	0.019	0.040	0.007	0.349
Collector-gatherer (Abd)	-12 (9)	67 (8)	41 (12)	0.000	0.001	0.000	0.091
Terrestrial Invertebrates (Biom)	-32 (16)	33 (22)	19 (23)	0.083	0.080	0.041	0.641
Negative response to clearcuts							
Shredders (%)	26 (14)	-56 (9)	-27 (19)	0.015	0.030	0.007	0.291
Total Taxa diversity density	-7 (8)	-18 (8)	-31 (8)	0.114	0.040	0.350	0.290
Positive response to old clearcuts							
Ephemeroptera (Abd)	-22 (9)	67 (16)	-5 (30)	0.026	0.550	0.009	0.033
Ephemeroptera (Biom)	6 (11)	77 (11)	-25 (35)	0.028	0.310	0.052	0.009
Collector Gatherer (%)	1 (5)	61 (13)	13 (11)	0.002	0.388	0.001	0.003
Scraper (Biom)	-35 (20)	73 (11)	27 (40)	0.098	0.139	0.045	0.373
Clinger diversity density	-15 (10)	36 (23)	-7 (14)	0.088	0.716	0.038	0.074
Collector-gatherer (Biom)	-14 (14)	69 (11)	24 (22)	0.014	0.123	0.004	0.090
Positive response to new clearcuts							
Aquatic inverterbate (Biom)	-16 (18)	19 (23)	43 (16)	0.086	0.029	0.210	0.388
Old clearcuts >> New clearcuts							
Ephemeroptera (%)	8 (14)	60 (19)	-18 (31)	0.104	0.409	0.138	0.037

Note: Level of significance is considered p = 0.05
Abd = abundance, Biom = biomass; Control n=8, Old n=6, New n=8.

We now describe our findings for each set of biotic metrics following the order they were introduced in Table 4. When referring to the significance for biotic metric comparisons among treatments, we are referring to effect (Equation 3) and not to the raw biotic metrics presented previously in Tables 6 and 7. Note that the level of significance is set at α=0.050, and the actual p values are listed in Table 8 for each biotic metric (effect) that significantly differs in at least one comparison.

Invertebrate abundance, invertebrate biomass, and aquatic invertebrate abundance significantly differed between controls and each clearcut group (Fig. 15). Aquatic invertebrate biomass differed only between control and new clearcuts. Old and new clearcut treatment effects did not differ for any of these variables. The magnitude of each effect for total invertebrate and aquatic invertebrate densities increased from control, to old, to new clearcuts. Terrestrial invertebrate abundance density did not differ significantly among or between treatments. Terrestrial biomass density tended to be higher in both clearcut groups, and the largest effect occurred in old clearcuts, which differed significantly from the control group (Fig. 15).

Ephemeroptera abundance and biomass density effects were both over 60 % in old clearcuts compared to nearly or less than 0 in controls and new clearcuts (Fig. 16). Ephemeroptera density differed between controls and old clearcuts for abundance ($p<0.050$) and biomass ($p=0.052$), and differed between old and new clearcuts for both measures ($p<0.050$). Plecoptera and Trichoptera densities did not differ among treatments, but Diptera densities (abundance and biomass) differed between controls and both clearcut groups. Old and new clearcut effects were very similar, approximately 50%, compared to control effects of nearly 0. The combined measures of EPT and EPT/D did not differ significantly among treatment groups (Fig. 17).

Predator, collector-filterer, and shredder densities did not differ significantly among or between treatments (Fig. 18). Collector-gatherer abundance density differed significantly between controls and both clearcut groups, whereas biomass density differed only between control and old clearcuts (Fig. 18). Neither variable differed significantly between clearcut groups. Scraper biomass differed between control and old

clearcuts, with an effect of approximately 75 % in old clearcuts compared with –40 % in the control group, whereas scraper abundance density did not differ.

Percentage of aquatic and terrestrial invertebrates and percentage of the orders Plecoptera, Trichoptera, and Diptera did not differ among or between treatments (Fig. 19). Percent Ephemeroptera differed between old and new clearcuts, with the largest effect in old clearcuts. Among percentages of functional feeding groups, collector-gatherers differed between control and old clearcut groups, and between new and old clearcuts (Fig. 20). The greatest effect occurred in old clearcuts (61 %), with controls and new clearcuts showing a near 0 effect. Percent shredders differed between control and both clearcut groups, and did not differ between clearcut groups (Fig. 20). Contrary to all effects described thus far, percent shredders declined in both clearcuts compared to the control group. Effects of the remaining biotic indicators, percentage of clingers, non-insects, long-lived taxa and intolerant taxa, and the Hilsenhoff Biotic Index, did not differ among or between treatments.

Total taxa diversity density responded negatively to new clearcuts but there was not a significant difference between effect in old clearcuts and controls (Fig. 21). Effect in old and new clearcuts also did not differ significantly. Clinger diversity density responded positively to old clearcuts and did not differ between control and new clearcuts, or between clearcut groups (Fig. 21). The remaining effects for diversity, heterogeneity, and evenness measures did not differ among or between treatments.

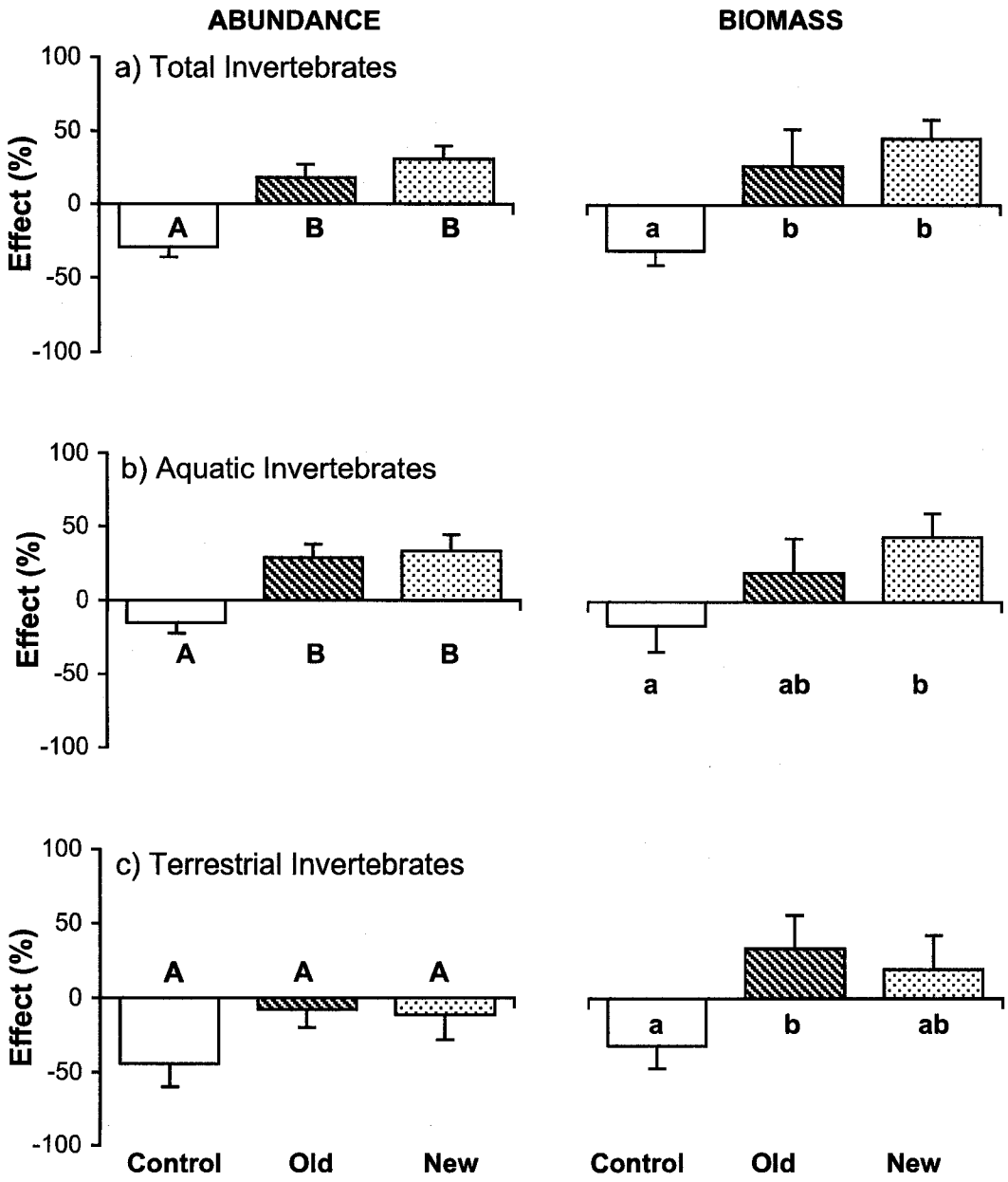

Figure 15. Densities of (a) total invertebrates, (b) aquatic invertebrates, and (c) terrestrial invertebrates found in control, new and old clearcut drift samples in Bone and Damfino Creek study areas. Abundance densities are on the left, biomass densities are on the right. Control mean effects are open columns (n=8), old clearcuts are hatched (n=6), new clearcuts are grey (n=8), and error bars represent SEM. A positive effect indicates that drift densities increased from the upstream to downstream sites. Means that share a letter do not differ significantly ($p>0.05$).

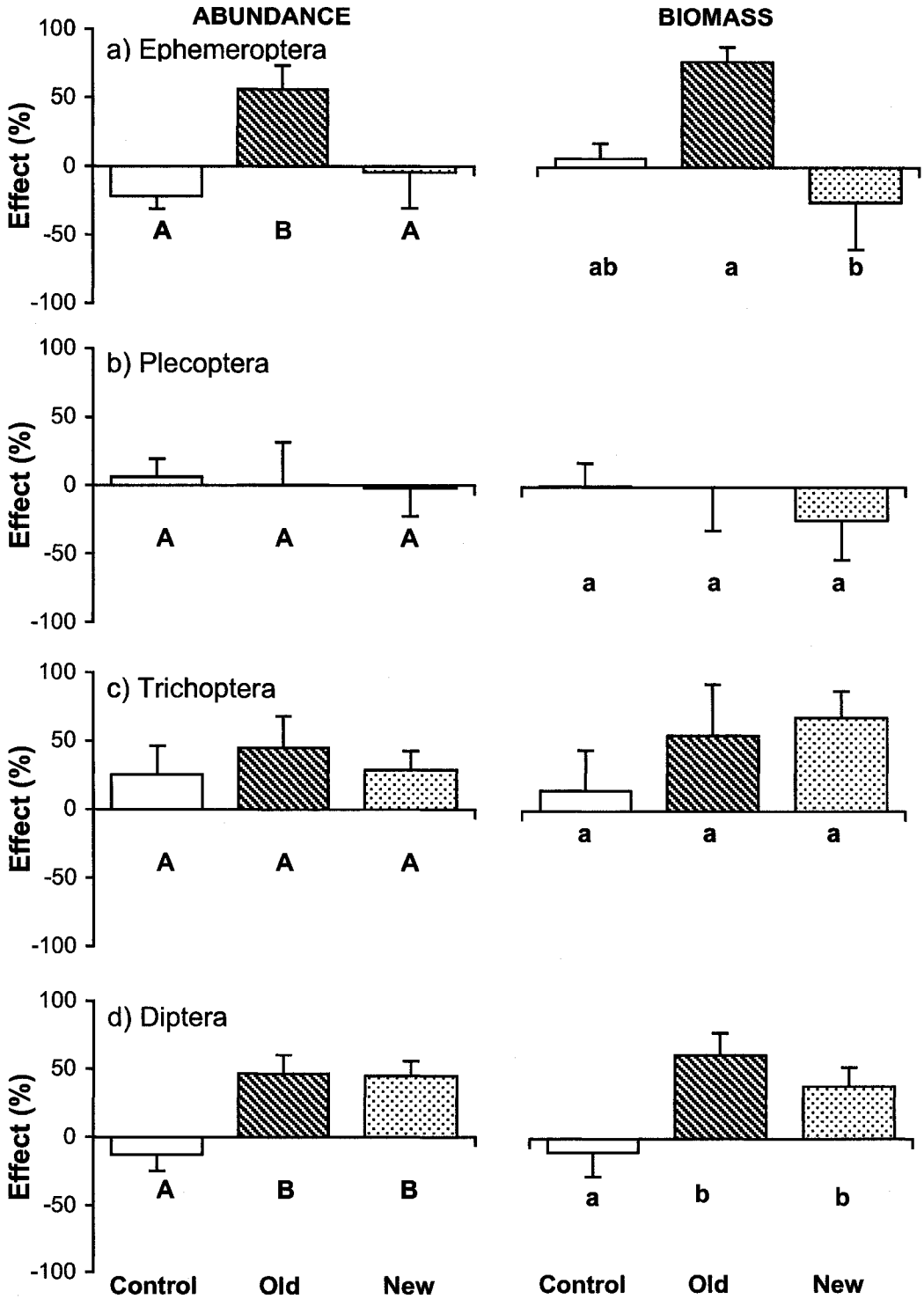

Figure 16. Densities of (a) Ephemeroptera, (b) Plecoptera, (c) Trichoptera, and (d) Diptera found in control (n=8), old (n=6) and new (n=8) treatment drift samples in 2004. Abundance densities are on the left, biomass densities are on the right. A positive effect indicates drift densities increased from the upstream to downstream sites. Error bars represent SEM. Means that share a letter do not differ significantly ($p>0.05$).

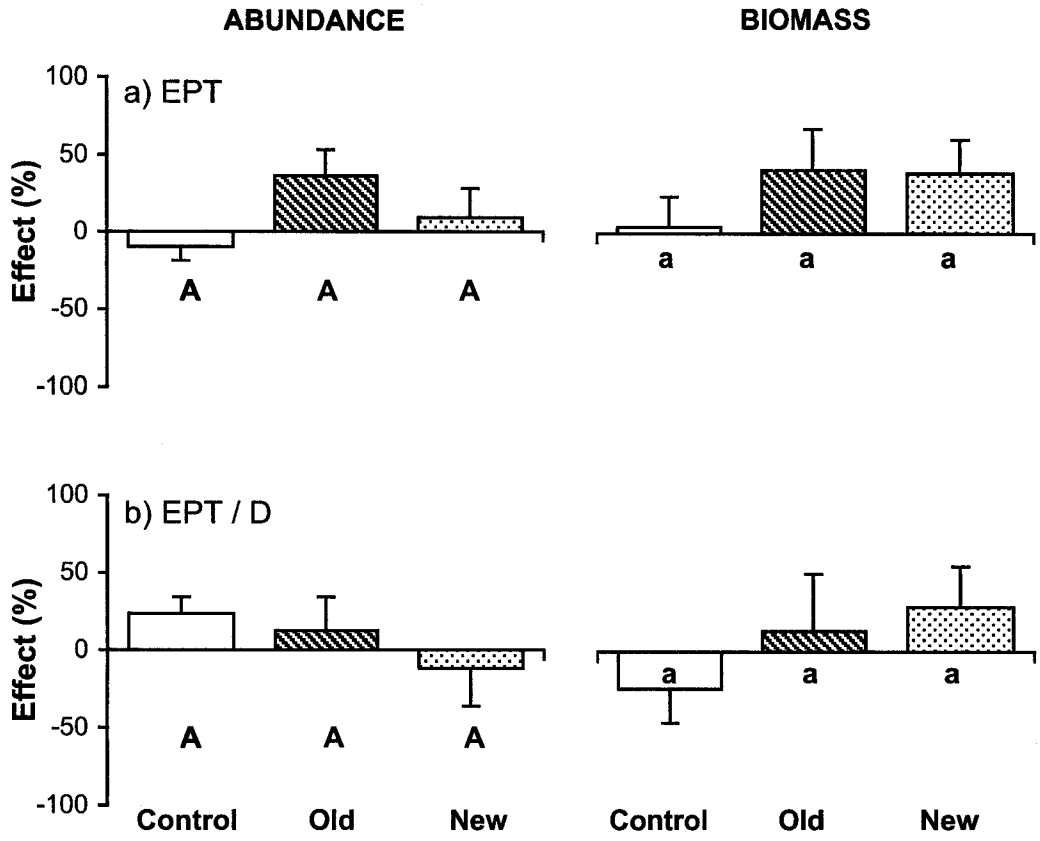

Figure 17. Densities of (a) EPT and (b) EPT/D found in control (n=8), old (n=6) and new (n=8) treatment drift samples in Bone and Damfino Creek study areas. Error bars represent SEM. Abundance densities are on the left, biomass densities are on the right. A positive effect indicates that drift densities increased from the upstream to downstream sites. Means that share a letter do not differ significantly ($p>0.05$).

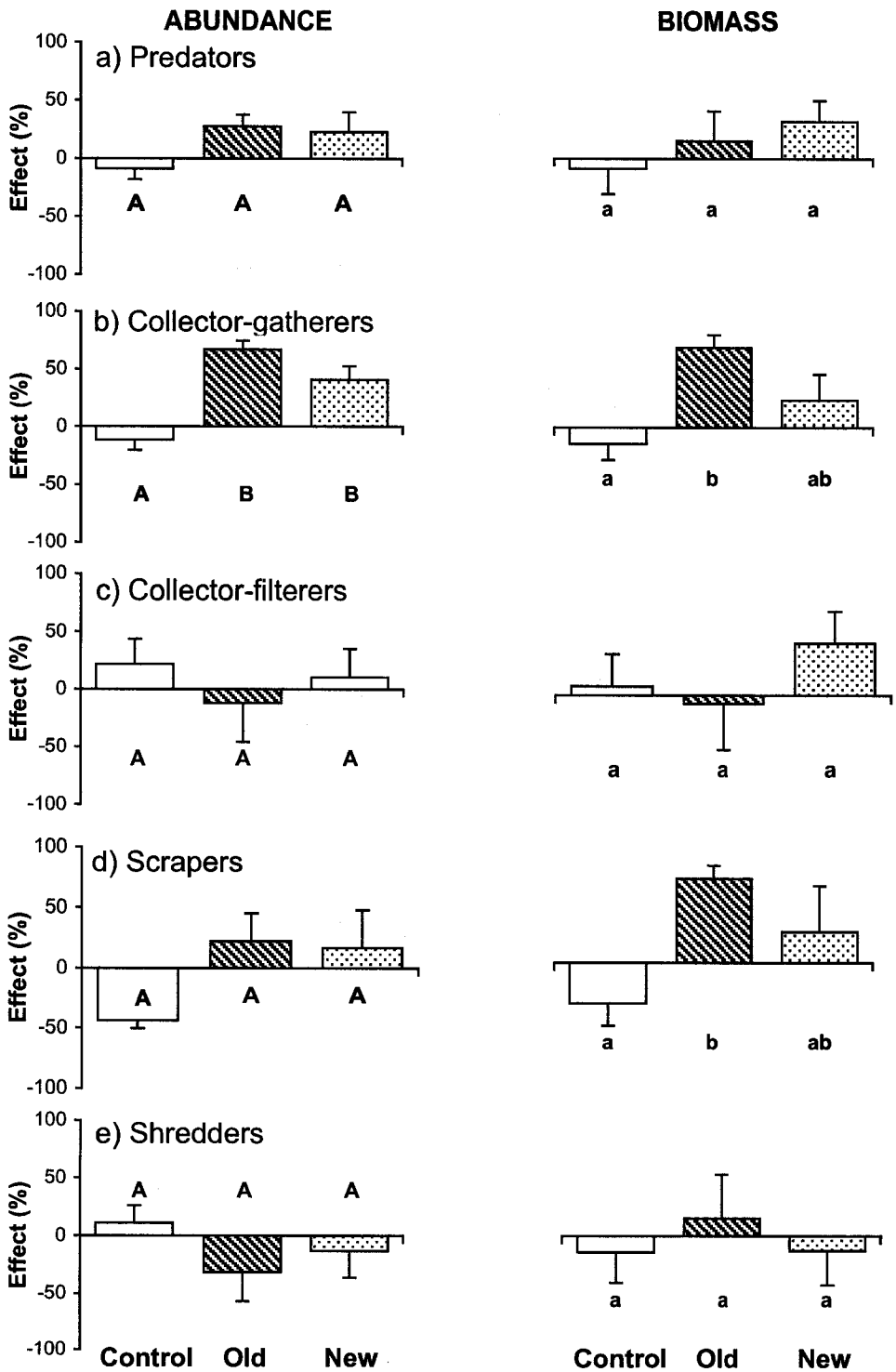

Figure 18. Densities of (a) predators, (b) collector-gatherers, (c) collector-filterers, (d) scrapers, and (e) shredders in control (n=8), old (n=6) and new (n=8) drift samples in Bone and Damfino Creek. Abundance densities are on the left, biomass densities are on the right. Positive effect indicates that drift densities increased from upstream to downstream sites. Means that share a letter do not differ significantly ($p>0.05$). Error bars represent SEM.

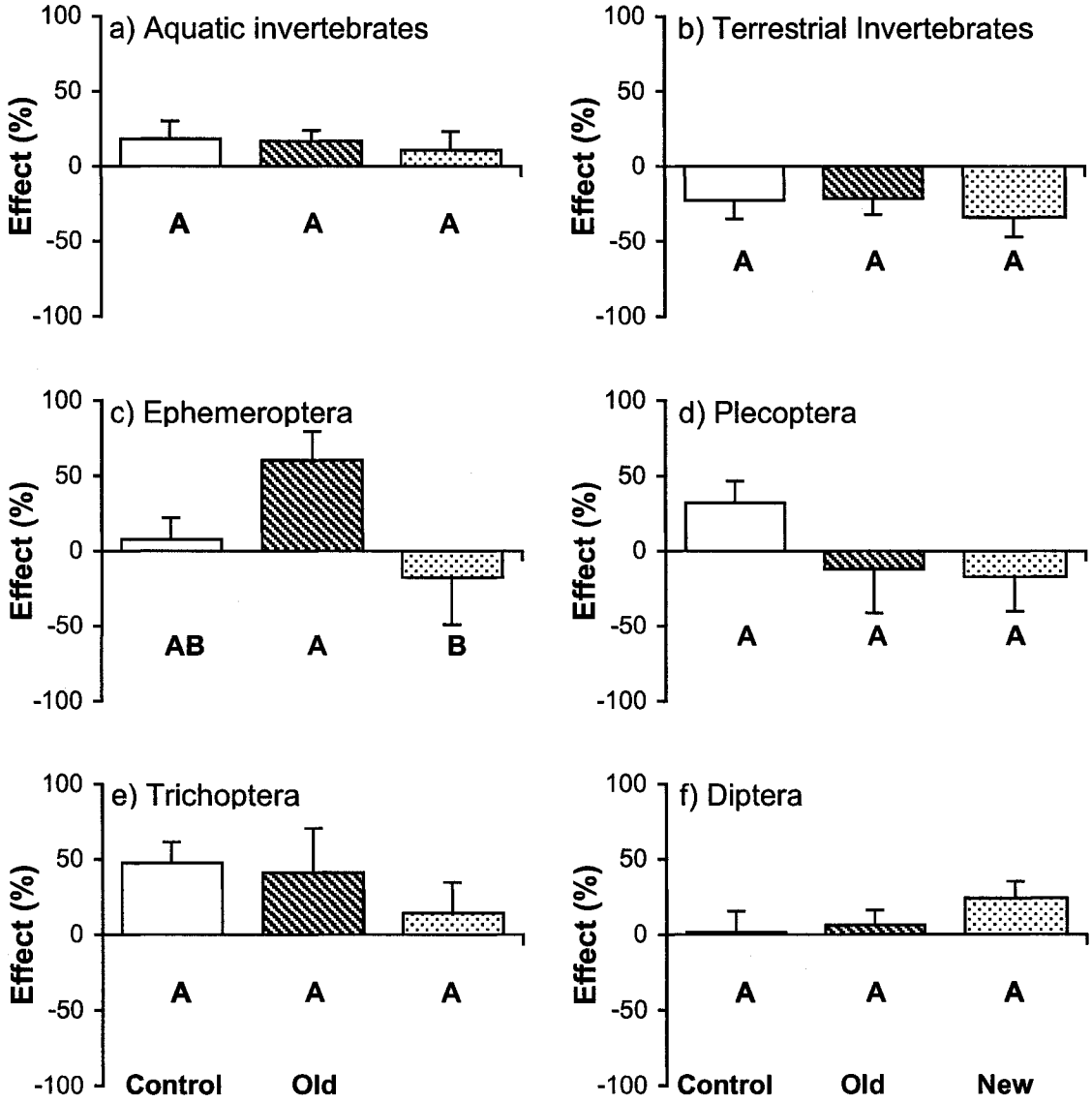

Figure 19. Percentage of total invertebrates made up of (a) aquatic invertebrates, (b) terrestrial invertebrates, (c) Ephemeroptera, (d) Plecoptera, (e) Trichoptera, and (f) Diptera in control (n=8), old (n=6) and new (n=8) treatment drift samples in Bone and Damfino Creek study areas. Error bars represent SEM. A positive effect indicates that drift densities increased from the upstream to downstream sites. Means that share a letter do not differ significantly ($p>0.05$).

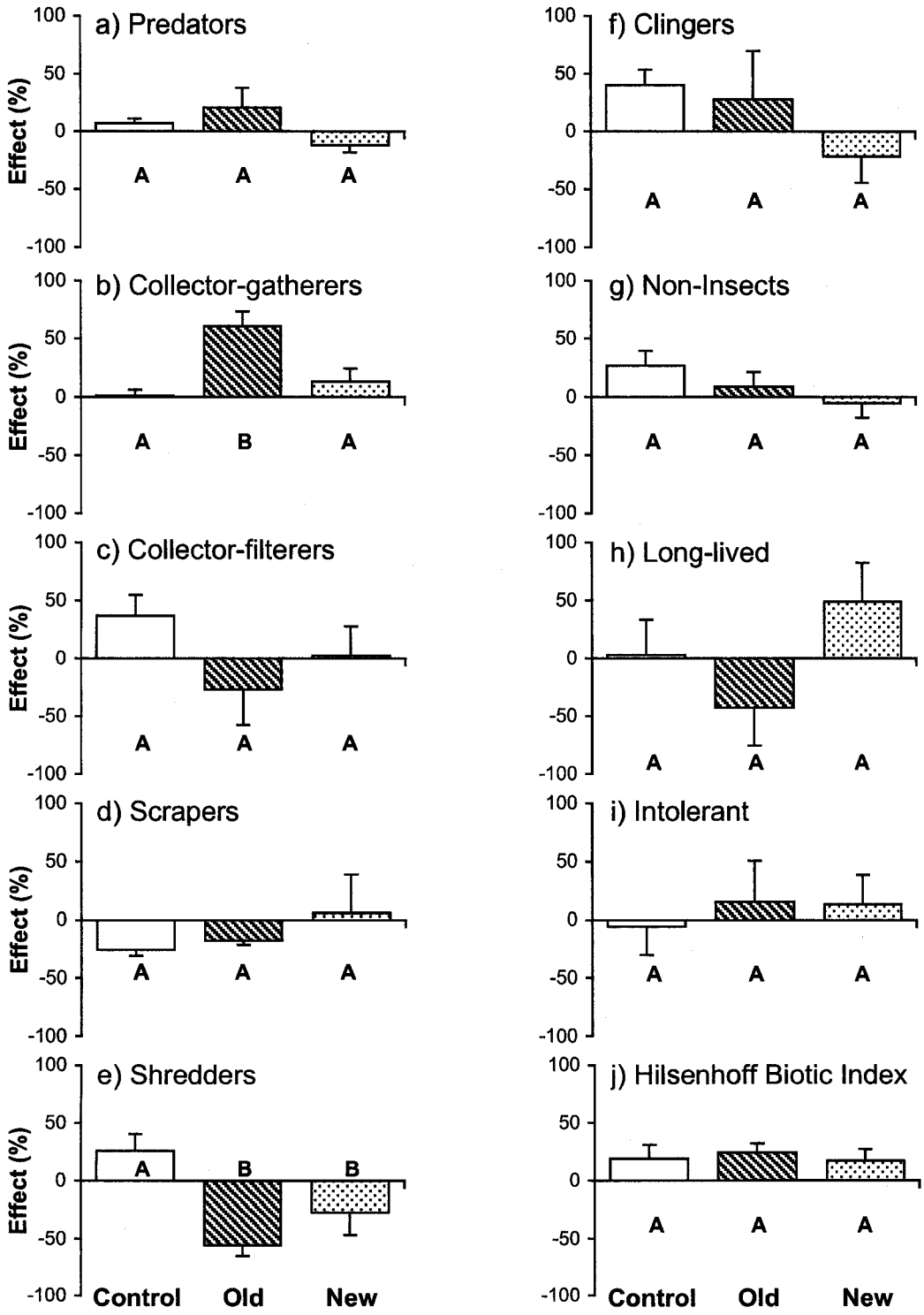

Figure 20. Percentage of groups by abundance, followed by a biotic index in control (n=8), old (n=6) and new (n=8) treatment drift samples in 2004. Groups are: (a) predators, (b) collector-gatherers, (c) collector-filterers, (d) scrapers, (e) shredders, (f) clingers, (g) non-insects, (h) long-lived, and (i) intolerant. Biotic index is (j) Hilsenhoff Biotic Index. Positive effect indicates that drift densities increased from upstream to downstream sites. Means that share a letter do not differ significantly ($p>0.05$). Error bars represent SEM.

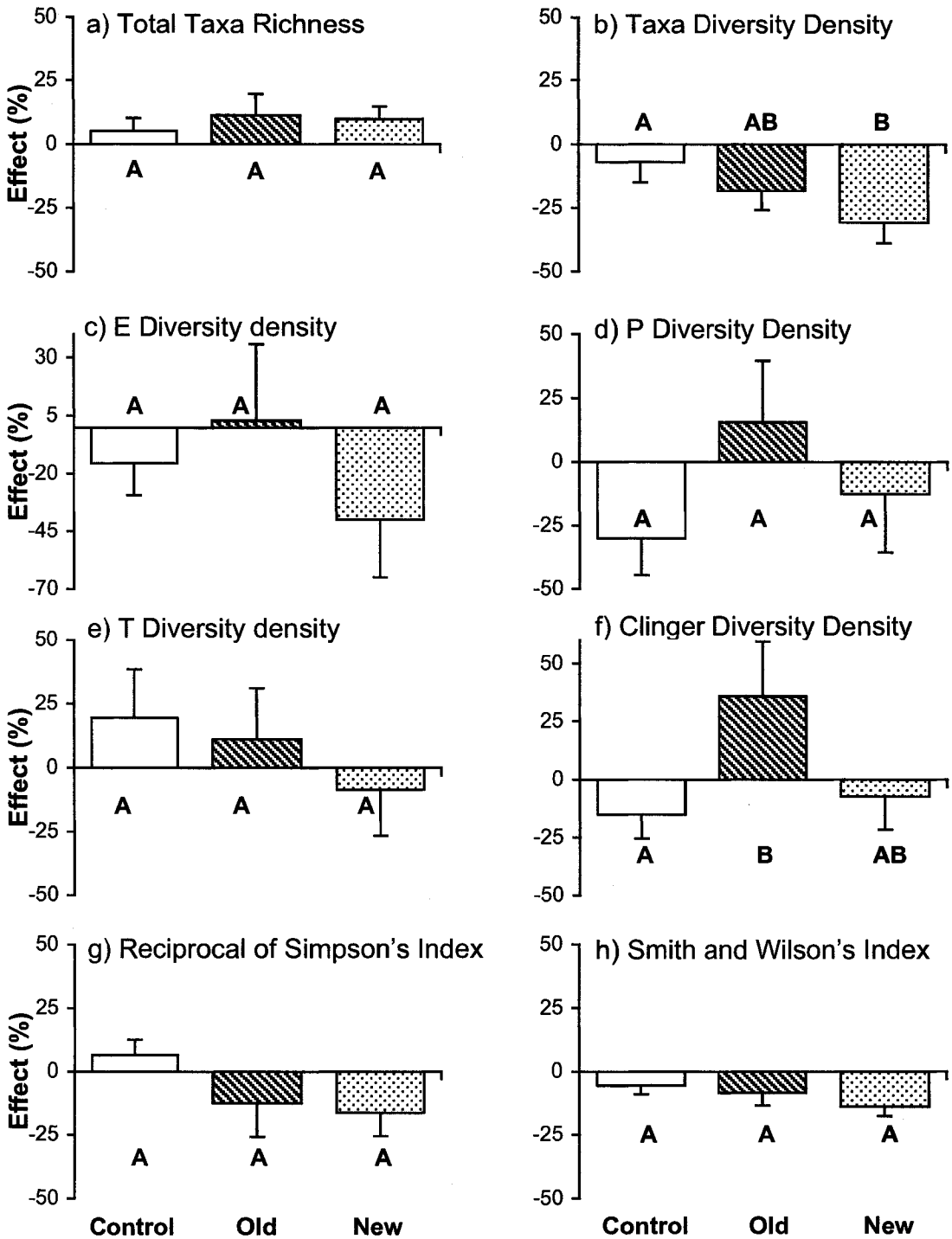

Figure 21. Mean effect among control (n=8), old (n=6) and new (n=8) treatment drift samples in 2004 of: (a) total taxa richness; taxa diversity density of the following groups: (b) total taxa, (c) Ephemeroptera, (d) Plecoptera, (e) Trichoptera, and (f) clingers; and biotic indices measuring: (g) heterogeneity, reciprocal of Simpson's index and (h) evenness, Smith and Wilson's index. Positive effect indicates that metrics increased from upstream to downstream sites. Means that share a letter do not differ significantly ($p>0.05$). Error bars represent SEM.

EPT Families and Genera

Among the orders Ephemeroptera, Plecoptera and Trichoptera, we identified 18 families and 34 genera overall with differing representation between study areas (Table 9). In Bone Creek Ameletidae, Baetidae, Heptageniidae, Chloroperlidae, Nemouridae, Peltoperlidae, *Ameletus*, *Baetis*, *Cinygmula*, *Zapada*, and *Yoraperla* occurred as greater than 1 % of total invertebrate abundance. In Damfino Creek, Ameletidae, Chloroperlidae, Nemouridae, *Ameletus, Haploperla, Suwallia*, and *Podmosta* occurred as greater than 1% of total invertebrate abundance on average (Table 9). Two families, Ameletidae and Baetidae, were represented by one genus each (*Ameletus* and *Baetis*, respectively) and were, therefore, redundant in the analysis due to the family densities being identical to the respective genus.

We conducted 13 logistic regressions that all showed site location (upstream of or within clearcuts) did not predict presence/absence of common taxa. There were two analyses where standard error of the beta coefficient for site location was greater than 2.0, indicating problems such as all cases having the same value or complete separation. Examination of these taxa, Nemouridae and *Zapada* in Bone Creek, revealed two important points. First, their presence/absence data were identical as *Zapada* made up the majority of the family. Second, presence/absence data showed nearly all cases had the same value, as *Zapada* occurred in all clearcut sites except one new and one old downstream site. The remaining 11 logistic regressions were not significant with Damfino Creek p values for overall model fit ranging from 0.614 – 1.00, and Bone Creek p values ranging from 0.244 – 0.557.

To meet the assumptions of linear regression, we examined standardized residuals to assess outliers, and excluded cases with values between -3.3 and 3.3 (Tabachnick and Fidell 1989). This occurred only in regressions that were not significant, and excluding outliers did not change their results. We assessed scatterplots of residuals and found the assumptions of normality, linearity, and variances evenly distributed along the range of the dependent variables were met in all except two regressions. Residuals for Nemouridae in Damfino Creek were not normally distributed. We applied logarithmic and square root transformations recommended for abundance data (Rosenberg and Resh 1993), but they did not improve the distributions and therefore we proceeded with untransformed variables. Tolerance values approached 1 showing singularity between independent variables.

Of the 15 linear regressions using DOC and FPOM (PCA components 1, 2) entered together, two models were significant. In Bone Creek, Chloroperlidae abundance was significantly related to organic matter that explained 31 % of its variance ($F_{2,17}$=3.744, p=0.045). Within the model, DOC was not significant but FPOM contributed significantly to the model (t=2.634, p=0.017). The model did not improve appreciably by removing DOC (adjusted R^2=0.31, p=0.012). Organic matter predicted abundance of *Ameletus* in Damfino Creek ($F_{2,21}$=3.568, p=0.046), with FPOM contributing significantly to the model (t=2.431, p=0.024). The model improved by removing DOC, and FPOM explained 25 % of the variance in *Ameletus* (p=0.014). There were positive relationships between the independent variable representing FPOM concentration, and abundance of Chloroperlidae and *Ameletus* in Bone Creek and Damfino Creek study areas, respectively (Fig. 22).

Table 9. Representation of EPT families and genera among treatments in drift samples at Bone Creek and Damfino Creek study areas. Dots indicate presence of genera listed under each family.

		BONE CREEK							Damfino Creek						
		mean % of drift	Control DS	Control US	Old DS	Old US	New DS	New US	mean % of drift	Control DS	Control US	Old DS	Old US	New DS	New US
E	Ameletidae	1.8							1.6						
	Ameletus	1.8	●	●		●	●	●	1.6	●	●	●	●	●	●
	Baetidae	2.6							0.1						
	Baetis	2.6	●	●	●		●	●	0.1	●					
	Ephemerellidae	0.3							0.03						
	Attenella	0.05	●						0						
	Drunella	0.02	●						0.03		●				
	Heptageniidae	1.1							0.2						
	Cinygmula	1.0	●	●	●		●	●	0.02		●				
	Epeorus (Iron)	0.2	●	●	●		●		0						
	Epeorus (Ironopsis)	0.1	●	●			●		0						
	Rhithrogena	0.01		●					0						
P	Chloroperlidae	1.0							3.5						
	Haploperla	0.2		●		●	●	●	1.5	●	●	●	●	●	●
	Suwallia	0.4	●	●		●	●	●	1.3	●	●	●	●		●
	Sweltsa	0.1	●			●	●	●	0						
	Leuctridae	0.5							0						
	Despaxia	0.5	●	●	●	●	●	●	0						
	Nemouridae	3.9							9.4						
	Podmosta	0.03				●			9.3	●	●	●	●	●	●
	Zapada	3.2	●	●	●	●	●	●	0.04	●			●		
	Peltoperlidae	1.9							0.1						
	Yoraperla	1.0	●	●	●	●	●	●	0.01	●					
	Soliperla	0.03		●					0						
	Perlodidae	0.2							0.8						
	Setvena	0.2				●		●	0						
	Taeniopterygidae	0.01		●					0						
T	Apataniidae	0.3							0.1						
	Allomyia	0.1	●				●		0.1			●			
	Moselyana	0.2	●		●		●	●	0						
	Brachycentridae	0.1							0						
	Micrasema	0.1	●				●		0						
	Glossosomatidae	0.8							0						
	Glossosoma	0.7	●	●	●	●	●	●	0						
	Hydropsychidae	0.5							0						
	Parapsyche	0.1					●		0						
	Limnephilidae	0.7							0.5						
	Chyranda	0							0.1			●	●		
	Cryptochia	0							0.2			●	●		
	Desmona	0.2							0.03	●		●	●		
	Eocosmoecus	0.03		●					0						
	Homophylax	0.1			●				0						
	Onocosmoecus	0							0.01	●					
	Psychoglypha	0.2					●	●	0.1	●					
	Spagnophylax	0							0.01						●
	Philopotamidae	0.3							0.03						
	Wormaldia	0.3		●			●		0.03	●	●				
	Rhyacophilidae	0.5							0.1						
	Himalopysche	0.01		●					0						
	Rhyacophila	0.4	●	●	●	●	●	●	0.1		●	●	●	●	
	Uenoidae	0.2							0						
	Neothremma	0.2		●	●	●			0						

Note: Mean % of drift calculated using abundances at each site within study areas, treatments, and locations. US=upstream, DS=downstream site location. There are 4 streams in each category except Bone Creek old clearcuts where n=2. Indistinct specimens included in family numbers, adults (terrestrial) were excluded.

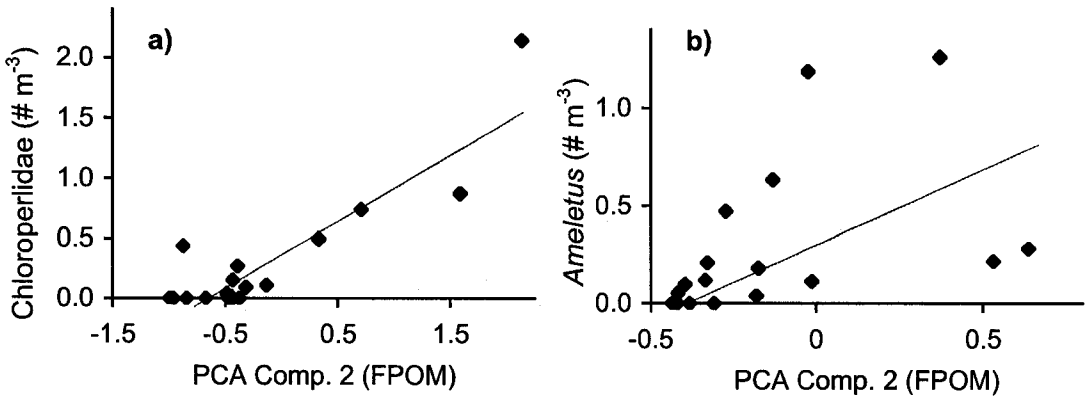

Figure 22. FPOM as PCA Component 2 was significantly related to (a) Chloroperlidae density at Bone Creek and (b) *Ameletus* density at Damfino Creek study area.

Discussion

Biotic Metrics

Mean drift of invertebrates in this study was 10-34 individuals m^{-3} and is in the mid-range of densities reported for other small streams throughout the world (0.02-143 individual m^{-3}, see Giller and Malmqvist 1998). In North America, our drift rates were comparable to an average 29 individuals m^{-3} found by Siler et al. (2001) in hardwood forested streams, and to 1-22 invertebrates m^{-3} reported by Wipfli and Gregovich (2002) in Alaska. Assuming discharge and drift were constant through 24 hours, our streams exported 652-3813 mg of invertebrates $stream^{-1}$ day^{-1} on average among treatment groups, compared to that reported in Alaska of 163 mg $stream^{-1}$ day^{-1} (Wipfli and Gregovich 2002). We only measured drift rates during the day in a season when drift was expected to be high coinciding with high discharge, whereas the other researchers sampled drift throughout the day and year. Although drift diel patterns are reduced in non-fish bearing streams, a pattern of increasing drift in late afternoon and evening is still expected (Smock 1996). Therefore, our densities represent minimum estimates of invertebrate drift during a high drift seasonal period. However, if invertebrate drift rates

that we reported were representative for the summer period, these headwater streams have the potential to subsidize downstream food webs considerably in the season when fish are generally food limited.

Total invertebrate drift responded positively to clearcuts within 1-3 years post harvest and did not recover within seven years post harvest. Our finding that overall drift increased is similar to the benthic invertebrate density responses to clearcut logging for the same time frame (Newbold et al. 1980; Webster et al. 1983; Noel et al. 1986; Stone and Wallace 1998; Hernandez et al. 2005). Increased drift corresponds directly with the findings of Wilzbach et al. (1986) who reported increased drift densities in clearcuts seven years post harvest in third order streams in Oregon. Our findings of the composition changes, discussed later, support that elevated primary production lead to increased macroinvertebrate production and increased drift during the seven year post harvest period that we examined in this study. In addition, the disturbed habitat likely favoured production of short-lived multivoltine taxa that further contributed to increased macroinvertebrate production (Gregory et al. 1987). An additional factor in our study is that alder (*Alnus sp.*) was a common deciduous species that was either left intact, or quickly regenerated adjacent to streams in both clearcut types. This affects invertebrate production in two ways. Alder has a faster processing rate than coniferous species or other deciduous species and can therefore supply more quality food to the stream food web (Cummins et al. 1989). Secondly, increased drift densities are associated with alder in the riparian zone. Wipfli and Musselwhite (2004) found that amount of red alder in the riparian zone was positively related to aquatic taxa in the drift, and Allan et al. (2003) reported that more terrestrial invertebrates tended to drop from red alder than hemlock and spruce vegetation. Both aquatic and terrestrial invertebrates drove increased drift in

clearcuts, and the percentage of both groups was not altered in response to clearcut treatments.

Terrestrial invertebrates are generally larger than aquatic invertebrates (Allan 1995), and this could explain why we detected a response in biomass of terrestrial invertebrates without detecting a response in abundance. Edwards and Huryn (1995) also found that although biomass of terrestrial invertebrates in the drift differed in response to land use, abundance of terrestrials did not. Drift feeding fish select terrestrial invertebrates due to their larger size and their differential availability compared to aquatic invertebrates on a seasonal and diel basis (Nakano et al. 1999). Terrestrial invertebrates comprise an important part of adult salmonid diets (Bridcut 2000; Kawaguchi and Nakano 2001; Allan et al. 2003); however, Bilby and Bisson (1992) attributed increased autochthonous inputs to increased production of juvenile coho salmon in headwater streams seven years following clearcutting. Wilzbach et al. (1986) found a strong correlation between trout growth and drift densities and reported short-term relative growth rates of trout in clearcut streams greatly exceeded that of reference streams. In the period up to seven years post harvest in the present study, clearcuts appeared to cause more aquatic invertebrates and larger terrestrial invertebrates to drift, both of which could lead to increased fish production.

Diptera abundance responded positively to both clearcut treatments, but maximum effect occurred in new clearcuts. Diptera biomass density showed the highest effect in old clearcuts. This effect is parallel to that of terrestrial invertebrates and the order Diptera was highly influenced by adults in the drift. While abundance of Diptera responded positively 1-3 years post harvest, a positive response of Ephemeroptera was delayed until 5-7 years following clearcutting. Both abundance and biomass of

Ephemeroptera had maximum effects in old clearcuts. These two groups of insects are reported to respond positively to disturbance in benthos, in part because they comprise short-lived taxa that are able to exploit disturbance (Wallace and Gurtz 1986, Gregory et al. 1987). For example, Noel et al. (1986) found that Ephemeroptera and Diptera drove 2-4 fold increases of benthic invertebrate density within three years post harvest. Three multivoltine taxa drove increased densities found by Newbold et al. (1980) 1-5 years following harvest in Northern Californian headwater streams. A shredder stonefly, *Nemoura,* showed the highest increased density and drove the elevated total benthic invertebrate density in combination with increases to Chironomidae (Diptera) and a collector-gatherer mayfly, *Baetis*. Because these taxa are able to colonize rapidly, they are able to increase densities rapidly and are therefore favoured in a disturbed habitat. Although the authors noted the shift to multivoltine taxa, they primarily attributed increased densities to a shift in food base resulting from increased light, nutrients and temperature following logging. These results correspond with Wallace and Gurtz (1986) who reported that initial increases and subsequent declines of *Baetis* density coincided with changes in primary production.

Percent shredders responded negatively to clearcuts while two other functional feeding groups, collector-gatherers and scrapers, responded positively to clearcuts. The response of shredders was negative in the first 1-3 years, and no recovery was found seven years post harvest. This finding agrees with Gurtz and Wallace (1984), who found declines in benthic shredder abundance five years post harvest. In the longer term, Stone and Wallace (1998) and Hernandez et al. (2005) found that shredder densities drove a positive response in overall invertebrate benthic densities in clearcuts compared to reference streams 16 and 35-45 years post harvest, respectively. In the present study,

increased non-shredder densities are partly responsible for the decrease in percent shredders, and overall shredder densities were not significantly altered in either clearcut treatment. The post harvest increase of shredders reported in benthic invertebrate research did not occur within seven years post harvest in the present study.

In several studies where invertebrate benthic densities increased in response to clearcutting, scraper and collector gatherer densities drove the response in the first 2-5 years post harvest (Webster et al. 1983, Gurtz and Wallace 1984, Hernandez et al. 2005). Each study attributed the response of these trophic groups to elevated primary production due to increased light, temperature and nutrients in clearcut streams. Our finding that the scraper effect only differed significantly from controls in clearcut streams 5-7 years and not 1-3 years post harvest is contrary to the findings of Gurtz and Wallace (1984), who found that scraper benthic densities declined five years post harvest. A possible explanation is that increased drift of scrapers resulted from degradation of their habitat in the old clearcut treatment. Siler et al. (2001) found that percent of benthos in the drift increased for detritivores in a habitat where detritus was removed; however, overall drift densities were higher in the reference conditions regardless of percent of benthos in the drift. In the present study, there was the tendency for scraper densities to increase in both clearcut groups, with effects of 73 % in old clearcuts and 27 % in new clearcuts, compared with –35 % in control streams. Scrapers made up the smallest percentage of the drift among functional feeding groups. Therefore, our ability to detect differences among treatments may have depreciated due to a number of zero counts among sites for this variable.

Collector-gatherer was the only functional feeding group that significantly differed in abundance, biomass, and percent of invertebrates measures calculated within

the drift samples. For each variable, maximum effect occurred in old clearcuts. This trend differed from total invertebrate, aquatic invertebrate, and Diptera abundance, but was parallel to Ephemeroptera abundance. The majority of Ephemeroptera taxa identified in our drift samples were collector-gatherers (6 of 11), including two common genera, *Ameletus* and *Baetis*, and the remainder were scrapers. Unlike Ephemeroptera abundance, response of collector-gatherers was significant for both clearcut groups. This illustrates that by examining the functional feeding groups we detected a more specific response than was possible using an order level biotic metric. We found that fine particulate organic matter increased in new clearcuts but recovered in old clearcuts, and this would specifically affect collector-gatherers. An additional consideration is that trophic groups have differing propensities to enter the drift. Collector-gatherers tend to be swimmers and sprawlers that more actively drift, whereas scrapers tend to be clingers and passively enter the drift (Merritt and Cummins 1996). Among the taxa we collected, collector-gatherers and collector-filterers had the least number of clinger taxa in their groups. Therefore, a change in the benthic density of collector-gatherers may be more readily detected in the drift than other groups.

Clinger diversity weighted for number of clingers in a sample significantly responded to old clearcuts. The standard errors in this variable were extremely high. In 13 of 44 sites clinger taxa did not occur and percent of clingers was low, ranging from 0.35 – 5.25 % among treatments (Table 7). It appears that our ability to detect differences in clinger diversity density may be limited due to their low occurrence and number of zero counts in the data. Benthic clinger diversity is predicted to decline with increased levels of disturbance (Karr and Chu 1999). Our result that diversity of clingers

increased in old clearcuts complements our findings that total taxa diversity density recovered in that treatment.

The density of taxa diversity showed a negative response to new clearcuts (Fig. 21b). Decreased taxa richness occurred in benthic bioassessment with increasing degree of disturbance (Fore et al. 1996; Karr and Chu 1999), and due to effects of clearcut logging (Quinn et al. 2004). Collier (1995) found that taxa richness was positively correlated with shade but not with proportion of native forest cover in the riparian zone. This corresponds with our finding assuming that shade increased in old clearcuts with regrowth of early successional vegetation. Conversely, Hernandez et al. (2005) did not find differences in taxa richness between five year old clearcuts and control streams. In the present study, taxa richness without weighting for number of organisms sampled did not differ among treatments (Fig 21). Gotelli and Colwell (2001) emphasize several notes of caution in using diversity density, and suggest careful consideration to determine the variable that best determines sampling intensity, for example time, number of organisms, or volume of water in the case of drift samples. Despite our efforts to achieve consistent sampling intensity by adjusting length of sampling time according to discharge of the streams, volume of the drift sample differed by up to an order of magnitude higher among the samples collected from the study sites. There was a wide range in numbers of organisms collected in samples, and the larger volume samples did not necessarily have the highest number of organisms. Examination of these data guided us to use number of organisms in each sample as the determination of sampling intensity, because the number of taxa identified tends to increase with number of individuals in a sample (Krebs 1999). Our results showing decreased taxa diversity density indicates decreased stream health

initially following clearcutting, and recovery with respect to this metric 5-7 years post harvest (Karr and Chu 1999).

The importance of considering taxa richness within each order, Ephemeroptera, Plecoptera, and Trichoptera was emphasized by Karr and Chu (1999) because taxa in these groups respond differently to disturbance, thus combining them masks their more specific responses. We did not detect significant responses for diversity density in each of these orders (Fig. 21). Ephemeroptera, Plecoptera, and clinger diversity density effects showed a trend of positive response in old clearcuts. Trichoptera diversity density showed a similar trend to taxa diversity density, with most significant negative effects in new clearcuts, and intermediate values in old clearcuts. Our ability to detect differences in these biotic metrics may have been hampered by the patchy distribution of EPT among drift samples. Plecoptera occurred as 12 % of the drift, Ephemeroptera as 7 %, and Trichoptera as 4 % of the drift on average among all sites. Even by pooling replicate samples at each site, 10 of 44 sites did not contain Ephemeroptera, three did not contain Plecoptera, and nine did not contain Trichoptera. This would cause numerous zero counts through the data set, and would decrease the likelihood of detecting a difference among treatments. Even though we did not detect significant differences, the results of two differing trends among the orders supports our previous arguments that differing responses to clearcut logging occurred in 1-3 year old versus 5-7 year old clearcuts.

Other measures of the community composition such as the indices of heterogeneity and evenness did not respond to clearcut treatments and mean effects showed similar values among treatments (Fig. 21 g,h). A related index, Shannon diversity, was greater in benthos of clearcut streams 35-45 years post harvest, but similar to reference streams five years post harvest (Hernandez et al. 2005). Newbold et al.

(1980) found that Shannon diversity decreased in stream 1-5 years following logging. We chose the reciprocal of Simpson's index rather than Shannon diversity to describe heterogeneity in order to weight common species more than rare species in our analysis (Krebs 1999). Reciprocal of Simpsons (1/D) varies from 1 to the number of species in a sample and is interpreted as the number of equally common species in a community. Like 1/D, Shannon diversity (H') increases with increasing number of species in the community. Unlike benthic samples, drift samples do not represent the entire community of invertebrates and it appears the responses to logging do not alter the heterogeneity or evenness of the community within the drift.

EPT Families and Genera

Site location did not predict presence/absence of families and genera among clearcut sites. Examining the presence/absence of EPT taxa between site locations among treatments (Table 9) revealed no clear patterns with the possible exception of Trichoptera taxa in Bone Creek. More Trichoptera taxa were identified in downstream than upstream samples of both old (ds=5, us=3) and new (ds=8, us=4) clearcuts compared to five taxa identified in downstream sites and six taxa in upstream sites of control streams. However, in control streams different taxa were present depending on site location in all three orders, but especially in Trichoptera of both study areas. This variation may be dependent on differences between site location such as elevation, or time of day that site locations were sampled, or may be due to natural variability among sites. In any case, high variability reduced our ability to detect differences in presence/absence of taxa dependent on clearcutting.

Abundance of Chloroperlidae at Bone Creek, and *Ameletus* at Damfino Creek were positively related to FPOM concentration. We found that FPOM concentrations

responded positively to new clearcuts. Considering that abundances of some common taxa were dependent on FPOM concentrations, this may in part explain the highest effect of invertebrate drift in new clearcuts. *Ameletus* are collector-gatherers and are linked to FPOM as a primary food source. One explanation for the relationship not occurring in Bone Creek is that FPOM concentrations were generally higher in that study area whereas in Damfino Creek FPOM concentrations may have been in the range that would be more limiting as a resource. Both genera of Chloroperlidae that occurred in drift samples were predators. Murphy and Hall (1981) reported that predator benthic density increased in response to clearcuts five and more years post harvest, and attributed the effect to increased prey through elevated primary production. Hawkins et al. (1982) reported a significant correlation between benthic densities of predators and collector-gatherers in riffles. Another possible explanation is that drift density of Chloroperlidae, which are clingers, was related to FPOM concentration physically causing invertebrates to drift. This phenomenon was reported by Culp and Davies (1983), where negative pressure created by increased suspended particles caused invertebrates to enter the drift.

Experimental Approach

There were limitations to the present study. This is exemplified by several metrics that had distinct negative or positive values in control streams. Before-After Control-Impact (BACI) design and comparative surveys also have their limitations in aquatic research due to high natural variability among individual streams. In this design we used paired sites on streams upstream and within disturbance, but also established a base condition using paired sites on undisturbed streams. We recognize that differences between paired sites may occur independent of disturbance due to factors that may depend on elevation such as amount of light, water temperatures, and amount of canopy

closure. In addition, drift has diel patterns that, although subtle, still prevail in non-fish bearing streams (Smock 1996). We chose to consistently sample downstream sites in the morning and upstream sites in the afternoon. The effect of terrestrial and aquatic invertebrate contributions to the drift reflect this timing of our sampling given known diel differences in these variables. In all treatments, percent aquatics in downstream sites exceeded upstream sites, and percent terrestrials in upstream sites exceeded that of downstream sites. Drift of aquatic invertebrates tends to peak just before dawn and decrease throughout the day, opposite to the diel drift patterns of terrestrial taxa (Nakano et al. 1999). In control streams, the percentage of scrapers in the drift was higher at upstream than downstream sites, while the remaining functional feeding group percentages were either higher at downstream sites or were similar between sites. This may be the result of more light reaching streams at higher altitudes due to less canopy closure on approaching the alpine. This may also lead to increased productivity at upstream sites that accounts for the observed higher densities of invertebrates at upstream versus downstream sites of control streams (Fig. 15).

Implications and Summary

Logging can increase the trophic resources for drift-feeding fish such as salmonids if they are food limited (Bilby and Bisson 1992; Hetrick et al. 1998). There are several ways that invertebrate responses to logging adjacent to headwater streams may achieve this. Increased light, temperature and nutrients following clearcut logging stimulates increased benthic invertebrate production. The taxa that drive increased benthic densities following clearcutting are those that tend to drift (Newbold et al. 1980; Noel et al. 1986). Although allochthonous resources may be reduced, lignin-based leaf litter from coniferous trees have a higher ratio of C:N and require further breakdown by

microbes to provide the same food quality to macroinvertebrates as autochthonous resources supply immediately (Murphy and Meehan 1991). This shift may transfer up the food web positively because at least one salmonid species, coho salmon, appears to consume primarily autochthonous food sources (Bilby and Bisson 1992). The drift densities we reported indicate that headwater streams in ESSF forests in British Columbia export significant amounts of invertebrate drift to downstream fish habitat.

Drift more accurately estimates prey availability than benthos and is positively correlated with fish production (Wilzbach et al. 1986). Our results indicated that clearcut logging up to seven years post harvest caused increased macroinvertebrate drift densities. By not altering the contribution of aquatic versus terrestrial invertebrates, clearcut logging did not adversely alter the composition of the drift with respect to fish production. Our results showed that other changes in community composition occurred. Some alterations were detected 1-3 years post harvest, while others onset 5-7 years following harvest. A number of alterations persisted through the 5-7 year post harvest period. We have used a number of biotic metrics to assess relative differences in invertebrate drift and numerous metrics enabled detection of differences among treatments. We caution against considering the metrics independently but do make inferences based on the group of responses that we detected. It is apparent from these responses that composition of the invertebrate community was altered up to seven years post harvest. Although short-term gains in number and biomass of invertebrates drifting in headwater streams are apparent from these data, clearcut logging altered the composition of invertebrate drift that persisted at least seven years post harvest. Both responses are concerns for fisheries management, and the longer-term effects of clearcut logging on export from headwater streams requires further consideration.

Epilogue

There are several linkages between the responses we found in FPOM and DOC, and those of invertebrate drift. Total invertebrate drift responded positively to both post-harvest periods but was greatest in new clearcuts, partly following the response of FPOM that increased in new clearcuts. Collector-gatherers directly consume FPOM and this functional feeding group made up the majority of invertebrates in drift samples. In addition to this connection, collector-gatherer taxa were shown to derive at least 20 %, and up to 100 % of their carbon from bacteria (Hall and Meyer 1998). Bacteria are known to respond rapidly to changes in DOC (Kreuztweiser and Capell 2003), in particular labile DOC of low molecular weight that is generally autochthonous (Allan 1995). Although the number of collector-gatherers responded positively to both "new" and "old" clearcut groups, positive responses in biomass and percent only occurred in old clearcuts. The latent positive responses of this group to old clearcuts may be in part, indirectly related to altered DOC composition.

The only other group to show a significant positive response was the scraper functional feeding group in response to old clearcuts; this suggests that scrapers responded to increased primary productivity that occurred in old clearcuts. Scraper densities and primary production responses normally occur in the initial years post harvest, rather than the delayed response that we observed. Our DOC results correspond with this finding. We inferred that increased autochthonous production in old clearcuts through the summer season caused the observed seasonal decline of SUVA in old clearcuts. The response in scraper densities indicated increased autochthonous production during the high flow season.

Results from the two approaches also showed different responses. Responses in organic matter were dominant in the 1-3 year post harvest period, whereas biotic metric responses occurred in both periods with a greater number of responses in the 5-7 year period. Removal of riparian vegetation primarily affects the macroinvertebrate community through increased light and alterations to detrital inputs. Although the quantity of organic matter may be greater in undisturbed streams, an increased proportion of higher quality autochthonous resources allows an increase in energy availability in small streams after canopy removal (Bilby and Bisson 1992). This shift may be delayed while fast processing streamside debris breaks down in the initial years providing a pulse of organic matter of lower nutritional quality. This boosts production overall, but the later onset of increased autochthonous production, inferred from the scraper response in old clearcuts, indicates onset of increased higher quality resource production was delayed.

Headwater stream ecosystems are a source for many downstream energy resources. Not only are the amounts of detritus and invertebrate drift important (Wipfli and Gregovich 2002), the source of these resources is of consequence because of its influence on nutritional quality and food web stability. Forested headwater streams may have more food web stability than larger reaches due to the dominance of allochthonous inputs or donor control (Woodward and Hildrew 2002), and the high number of weak trophic linkages (McCann et al. 1998). Therefore, although a shift from allochthonous to autochthonous resources induced by clearcut logging can result in increased production initially, trophic stability in small streams may be compromised.

This examination of the effects of changes in abiotic and biotic variables from clearcutting adjacent to headwater streams in ESSF forests is one of the only studies to

use these two approaches simultaneously in the interior of BC. The research provides baseline data that could be used for continued monitoring of small stream for fisheries or water quality management. The data contribute to a large body of research on effects of forest harvest on small streams and expand the knowledge base. In particular, this work expands knowledge for a forest type that is commercially and ecologically important but has previously been little studied. Additionally, we have examined numerous biotic metrics to compare drift samples, and highlighted drawbacks and different sensitivities in some of these indicators through our data. This contributes to a body of knowledge on use of biotic indicators for water quality monitoring. Each of these contributions strengthens decision making by either providing scientific knowledge on which to base decisions, or by developing scientific tools for monitoring stream health.

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Appendix

Table A1. List of taxa and their designations as aquatic (A), terrestrial (T), clinger (CLG=Y); in functional feeding groups predator (PR), collector-gatherer (CG), collector-filterer (CF), scraper (SC), shredder (SH); their Hilsenhoff biotic index value (HBI); and their status as tolerant (TOL=T), and long-lived (Long-lived=Y). Biomass formulas estimate dry mass (DM) in mg using body length (L) measurements.

Phylum	Class	Order	Family	Genus	Aqu. Terr.	CLG	PR	CG	CF	SC	SH	HBI	TOL	Long-lived	Biomass formula	Ref.	Note
Arthopoda	Entognatha	Collembola	n.s.		T			100				n.d.	n.d.	n.d.	DM=exp(-3.628)*power(L,2.494)	A	
Arthopoda	Arachnida	Araneae	Pisauridae	*Dolomedes*	A		100					n.d.	n.d.	Y	DM=exp(-3.106)*(power(L,2.929))	B	
Arthopoda	Arachnida	Acarina	n.s.	"egg-shape"	A		100					5			DM=exp(3.682)*(power(L,2.761))/1000	B	4
Arthopoda	Arachnida	Acarina	n.s.	"elongate"	A		100					5			DM=exp(3.682)*(power(L,2.761))/1000	B	4
Arthopoda	Arachnida	Acarina	n.s.	"brown/hard"	T		100					5			DM=exp(3.682)*(power(L,2.761))/1000	B	4
Arthopoda	Arachnida	Acarina	n.s.	"round"	A		100					5			DM=exp(3.682)*(power(L,2.761))/1000	B	4
Arthopoda	Arachnida	Acarina	Stygothrombidiidae	"elongate/soft"	A		100					5			DM=exp(3.682)*(power(L,2.761))/1000	B	4
Arthopoda	Arachnida	Araneae	n.s.		T		100					n.d.	n.d.	n.d.	DM=exp(-3.106)*(power(L,2.929))	B	
Arthopoda	Insecta	Coleoptera	Amphizoidae, ad		A	Y	100					1		Y	DM=exp(-3.460)*(power(L,2.790)	B	
Arthopoda	Insecta	Coleoptera	Carabidae		T	Y	100					n.d.	n.d.	n.d.	DM=0.0077*power(L,2.910)	B	
Arthopoda	Insecta	Coleoptera	Chrysomelidae, ad		T						100	n.d.	n.d.	n.d.	DM=exp(-2.427)*power(L,2.171)	A	
Arthopoda	Insecta	Coleoptera	Chrysomelidae		T	Y					100	n.d.	n.d.	n.d.	DM=.0392*(power(L,3.111))	D	
Arthopoda	Insecta	Coleoptera	Curculionidae, ad		T	Y					100	5			DM=exp(-3.460)*(power(L,2.790)	B	
Arthopoda	Insecta	Coleoptera	Dytiscidae, ad		A		100					5	T	Y	DM=.0618*power(L,2.502)	C	
Arthopoda	Insecta	Coleoptera	Dytiscidae		A		100					5	T	Y	DM=.0077*(power(L,2.910)	D	
Arthopoda	Insecta	Coleoptera	Elmidae, ad		A	Y		100				4		Y	DM=exp(-3.460)*(power(L,2.790)	B	
Arthopoda	Insecta	Coleoptera	Histeridae, ad		T							n.d.	n.d.	n.d.	DM=exp(-3.460)*(power(L,2.790)	B	
Arthopoda	Insecta	Coleoptera	Hydraenidae		T	Y	100					n.d.	n.d.	n.d.	DM=0.0077*power(L,2.910)	D	
Arthopoda	Insecta	Coleoptera	Hydrophilidae, ad		A			50		50		5		Y	DM=exp(-3.460)*(power(L,2.790)	B	
Arthopoda	Insecta	Coleoptera	Hydrophilidae		A		100					5		Y	DM=.0077*(power(L,2.910)	D	
Arthopoda	Insecta	Coleoptera	Staphylinidae, ad		T	Y	100					n.d.	n.d.	n.d.	DM=exp(-3.460)*(power(L,2.790)	B	
Arthopoda	Insecta	Coleoptera	Staphylinidae		T	Y	100					n.d.	n.d.	n.d.	DM=0.0077*power(L,2.910)	B	1
Arthopoda	Insecta	Coleoptera	n.s., ad		T							n.d.	n.d.	n.d.	DM=exp(-3.460)*(power(L,2.790)	B	
Arthopoda	Insecta	Coleoptera	n.s.		T							n.d.	n.d.	n.d.	DM=0.0077*power(L,2.910)	D	
Arthopoda	Insecta	Diptera	n.s., ad		T							n.d.	n.d.	n.d.	DM=exp(-3.293)*power(L,2.366)	B	
Arthopoda	Insecta	Diptera	Athericidae		A		100					2	T		DM=.0040*power(L,2.586)	D	
Arthopoda	Insecta	Diptera	Ceratopogonidae		A		100					6			DM=.0025*power(L,2.469)	D	
Arthopoda	Insecta	Diptera	Chironomidae		A		50	50				6			DM=.0018*power(L,2.617)	D	
Arthopoda	Insecta	Diptera	Culicidae		A			50	50			8	T		DM=.0025*power(L,2.692)	D	
Arthopoda	Insecta	Diptera	Dixidae		A			100				2			DM=.0025*power(L,2.692)	D	
Arthopoda	Insecta	Diptera	Empididae		A		100					6			DM=.0054*power(L,2.546)	D	
Arthopoda	Insecta	Diptera	n.s.									n.d.	n.d.	n.d.	DM=.0025*power(L,2.692)	D	
Arthopoda	Insecta	Diptera	Psychodidae		A			100				10			DM=.0025*power(L,2.692)	D	
Arthopoda	Insecta	Diptera	n.s., pu		A		50	50				6			DM=.0025*power(L,2.692)	D	5
Arthopoda	Insecta	Diptera	Sciomyzidae		A		100					n.d.	n.d.	n.d.	DM=.0025*power(L,2.692)	D	
Arthopoda	Insecta	Diptera	Simuliidae		A	Y			100			6			DM=.002*power(L,3.011)	D	
Arthopoda	Insecta	Diptera	Stratiomyidae		A			100				8	T		DM=.0025*power(L,2.692)	D	
Arthopoda	Insecta	Diptera	Syrphidae		A			100				10	T		DM=.0025*power(L,2.692)	D	

Phylum	Class	Order	Family	Genus	Aqu. Terr.	CLG	PR	CG	CF	SC	SH	HBI	TOL	Long-lived	Biomass formula	Ref.	Note
Arthopoda	Insecta	Diptera	Thaumaleidae		A	Y				100		11	I		DM=.0025*power(L,2.692)	D	
Arthopoda	Insecta	Diptera	Tipulidae		A			50			50	3			DM=.0029*power(L,2.681)	D	
Arthopoda	Insecta	Ephemeropter	n.s., ad		T							n.d.	n.d.	n.d.	DM=exp(-3.628)*power(L,2.494)	A	
Arthopoda	Insecta	Ephemeropter	Ameletidae	*Ameletus*	A			100				0			DM=0.0077*power(L,2.588)	D	
Arthopoda	Insecta	Ephemeropter	Baetidae	*Baetis*	A			100				5			DM=0.0033*power(L,3.196)	C	
Arthopoda	Insecta	Ephemeropter	Baetidae	n.s.	A			100				4			DM=0.0053*power(L,2.875)	D	
Arthopoda	Insecta	Ephemeropter	Ephemerellidae	*Attenella*	A	Y		100				2			DM=0.0103*power(L,2.676)	D	
Arthopoda	Insecta	Ephemeropter	Ephemerellidae	*Drunella*	A	Y		100				0			DM=0.0019*power(L,3.46)	D	
Arthopoda	Insecta	Ephemeropter	Ephemerellidae	n.s.	A	Y		100				1			DM=0.0103*power(L,2.676)	D	
Arthopoda	Insecta	Ephemeropter	Heptageniidae	*Cinygmula*	A	Y				100		4			DM=0.0108*power(L,2.754)	D	
Arthopoda	Insecta	Ephemeropter	Heptageniidae	*Epeorus (Iron)*	A	Y				100		0			DM=0.0056*power(L,2.926)	D	
Arthopoda	Insecta	Ephemeropter	Heptageniidae	*Epeorus (Ironopsis)*	A	Y				100		0			DM=0.0056*power(L,2.926)	D	
Arthopoda	Insecta	Ephemeropter	Heptageniidae	n.s.	A	Y				100		4			DM=0.0108*power(L,2.754)	D	
Arthopoda	Insecta	Ephemeropter	Heptageniidae	*Rhithrogena*	A	Y				100		0			DM=0.0108*power(L,2.754)	D	
Arthopoda	Insecta	Ephemeropter	ns.s		A							11			DM=0.0071*power(L,2.832)	D	
Arthopoda	Insecta	Hemiptera	n.s.		A		100					8			DM=exp(-3.308)*power(L,2.696)	B	
Arthopoda	Insecta	Hemiptera	Aphidae		T		100					n.d.	n.d.	n.d.	DM=exp(-3.308)*power(L,2.696)	B	
Arthopoda	Insecta	Hemiptera	Heteroptera (suborder)		T		100					n.d.	n.d.	n.d.	DM=exp(-2.998)*power(L,2.270)	B	
Arthopoda	Insecta	Hymenoptera	n.s., ad		T		100					n.d.	n.d.	n.d.	DM=exp(-3.871)*power(L,2.407)	B	4
Arthopoda	Insecta	Lepidoptera	n.s., ad		T						100	5			DM=power(exp,-5.036)*power(L,3.122)	A	
Arthopoda	Insecta	Lepidoptera	n.s.		T						100	5			DM=power(exp,-5.909)*power(L,2.959)	A	
Arthopoda	Insecta	Odonata	Anisoptera (suborder)		A		100					11		Y	DM=0.0078*power(L,2.792)	D	
Arthopoda	Insecta	Odonata	Zygoptera (suborder)		A		100					8			DM=0.0078*power(L,2.792)	D	
Arthopoda	Insecta	Plecoptera	n.s., ad	other	T							n.d.	n.d.	n.d.	DM=power(exp,-4.357)*power(L,2.539)	A	
Arthopoda	Insecta	Plecoptera	Chloroperlidae, ad		T							n.d.	n.d.	n.d.	DM=power(exp,-4.357)*power(L,2.539)	A	
Arthopoda	Insecta	Plecoptera	Chloroperlidae	*Haploperla*	A	Y	100					0			DM=.0065*power(L,2.724)	D	2
Arthopoda	Insecta	Plecoptera	Chloroperlidae	n.s.	A	Y	100					1			DM=.0065*power(L,2.724)	D	2
Arthopoda	Insecta	Plecoptera	Chloroperlidae	*Suwallia*	A	Y	100					0			DM=.0065*power(L,2.724)	D	2
Arthopoda	Insecta	Plecoptera	Chloroperlidae	*Sweltsa*	A	Y	100					1			DM=.0065*power(L,2.724)	D	2
Arthopoda	Insecta	Plecoptera	n.s.		A							11			DM=0.0094*power(L,2.754)	D	
Arthopoda	Insecta	Plecoptera	Leuctridae	*Despaxia*	A						100	0	I		DM=.0028*power(L,2.719)	D	3
Arthopoda	Insecta	Plecoptera	Nemouridae	n.s., ad	T							n.d.	n.d.	n.d.	DM=power(exp,-4.357)*power(L,2.539)	A	
Arthopoda	Insecta	Plecoptera	Nemouridae	n.s.	A						100	2			DM=.0056*power(L,2.762)	D	3
Arthopoda	Insecta	Plecoptera	Nemouridae	*Podmosta*	A						100	2			DM=.0056*power(L,2.762)	D	3
Arthopoda	Insecta	Plecoptera	Nemouridae	*Zapada*	A						100	2			DM=.0056*power(L,2.762)	D	3
Arthopoda	Insecta	Plecoptera	Peltoperlidae	n.s.	A	Y					100	1	I		DM=0.0170*power(L,2.737)	D	
Arthopoda	Insecta	Plecoptera	Peltoperlidae	*Soliperla*	A	Y					100	1	I	Y	DM=0.0170*power(L,2.737)	D	
Arthopoda	Insecta	Plecoptera	Peltoperlidae	*Yoraperla*	A	Y					100	1	I		DM=0.0170*power(L,2.737)	D	
Arthopoda	Insecta	Plecoptera	n.s., shredder		A	Y					100	11			DM=0.0094*power(L,2.754)	D	
Arthopoda	Insecta	Plecoptera	Perlodidae	n.s.	A	Y	100					2			DM=0.0196*power(L,2.742)	D	
Arthopoda	Insecta	Plecoptera	Perlodidae	*Setvena*	A	Y	100					2	I		DM=0.0196*power(L,2.742)	D	
Arthopoda	Insecta	Plecoptera	Taeniopterygidae	*n.s.*	A							2			DM=0.0094*power(L,2.754)	D	

Phylum	Class	Order	Family	Genus	Aqu. Terr.	CLG	PR	CG	CF	SC	SH	HBI	TOL	Long-lived	Biomass formula	Ref.	Note
Arthopoda	Insecta	Thysanoptera	n.s., ad		T							n.d.	n.d.	n.d.	DM=exp(-3.628)*power(L,2.494)	A	
Arthopoda	Insecta	Thysanoptera	n.s.		T							n.d.	n.d.	n.d.	DM=exp(-3.628)*power(L,2.494)	A	
Arthopoda	Insecta	Trichoptera	Apataniidae	*Allomyia*	A	Y				50	50	1	I		DM=0.0056*power(L,2.839)	D	
Arthopoda	Insecta	Trichoptera	Apataniidae	*Moselyana*	A			100				1	I		DM=0.0056*power(L,2.839)	D	
Arthopoda	Insecta	Trichoptera	Brachycentridae	*Micrasema*	A	Y		50			50	1			DM=0.0083*power(L,2.818)	D	
Arthopoda	Insecta	Trichoptera	Glossosomatidae	*Glossosoma*	A	Y				100		1			DM=0.0082*power(L,2.958)	D	
Arthopoda	Insecta	Trichoptera	Glossosomatidae	n.s.	A	Y				100		0			DM=0.0082*power(L,2.958)	D	
Arthopoda	Insecta	Trichoptera	Hydropsychidae	n.s.	A	Y			100			4			DM=0.0046*power(L,2.926)	D	
Arthopoda	Insecta	Trichoptera	Hydropsychidae	*Parapsyche*	A	Y			100			4			DM=0.0046*power(L,2.926)	D	
Arthopoda	Insecta	Trichoptera	Limnephilidae	*Chyranda*	A						100	1	I		DM=0.004*power(L,2.933)	D	
Arthopoda	Insecta	Trichoptera	Limnephilidae	*Cryptochia*	A					50	50	0	I	Y	DM=0.004*power(L,2.933)	D	
Arthopoda	Insecta	Trichoptera	Limnephilidae	*Desmona*	A						100	1	I	Y	DM=0.004*power(L,2.933)	D	
Arthopoda	Insecta	Trichoptera	Limnephilidae	*Eocosmoecus*	A						100	0	I	Y	DM=0.004*power(L,2.933)	D	
Arthopoda	Insecta	Trichoptera	Limnephilidae	*Homophylax*	A	Y					100	0	I	Y	DM=0.004*power(L,2.933)	D	
Arthopoda	Insecta	Trichoptera	Limnephilidae	n.s.	A							4			DM=0.004*power(L,2.933)	D	
Arthopoda	Insecta	Trichoptera	Limnephilidae	*Onocosmoecus*	A						100	1			DM=0.004*power(L,2.933)	D	
Arthopoda	Insecta	Trichoptera	Limnephilidae	*Pyschoglypha*	A	Y		50			50	0			DM=0.004*power(L,2.933)	D	
Arthopoda	Insecta	Trichoptera	Limnephilidae	*Spagnophylax*	A						100	4			DM=0.004*power(L,2.933)	D	
Arthopoda	Insecta	Trichoptera	Philopotamidae	*Wormaldia*	A	Y			100			3			DM=0.005*power(L,2.511)	D	
Arthopoda	Insecta	Trichoptera	n.s., pu		A							n.d.	n.d.	n.d.	DM=0.0056*power(L,2.839)	D	
Arthopoda	Insecta	Trichoptera	Rhyacophilidae	*Himalopysche*	A	Y	100					0	I		DM=0.0099*power(L,2.480)	D	6
Arthopoda	Insecta	Trichoptera	Rhyacophilidae	n.s.	A	Y	100					0			DM=0.0099*power(L,2.480)	D	6
Arthopoda	Insecta	Trichoptera	Rhyacophilidae	*Rhyacophila*	A	Y	100					0			DM=0.0099*power(L,2.480)	D	6
Arthopoda	Insecta	Trichoptera	Uenoidae	n.s.	A	Y		50		50		0			DM=0.0056*power(L,2.839)	D	
Arthopoda	Insecta	Trichoptera	Uenoidae	*Neothremma*	A	Y		50		50		0	I		DM=0.0056*power(L,2.839)	D	
Arthopoda	Insecta	Trichoptera	n.s.		A							n.d.	n.d.	n.d.	DM=0.0056*power(L,2.839)	D	
Arthopoda	Insecta	n.s.	n.s., terrestrial		T							n.d.	n.d.	n.d.	DM=exp(-3.628)*power(L,2.494)	A	
Mollusca	Gastropoda				A					100		7			afdm=.0203*power(L,2.521)	D	
Nematoda					A							5			DM=0.2679	E	
Nematomorpha					A							11			DM=0.2679	E	
Annelida	Clitellata				A			100				8			DM=0.025	E	6
Platyhelminthes	Turbellaria				A			100				4			DM=0.0082*power(L,2.168)	D	
Subphylum: Crustacea																	
Arthropoda	Branchiopoda				A				100			8			DM= 0.03300	E	
Arthropoda	Maxillopoda	Copepoda (Subclass)			A			100				8			DM= 0.03300	E	
Arthropoda	Ostracoda				A			100				8			DM=0.02644	E	

References

A. Sample et al. 1993, B. Rogers et al. 1977; C. Smock 1980; D. Benke et al. 1999; E. mean DM of at least 10 individuals taken from drift samples by C.A. Mackay in 2004.

Notes

1. Used designations for Staphylinidae adult.
2. Generally clingers, Merritt & Cummins (1996).
3. Sprawlers/clingers, Merritt and Cummins (1996).
4. These taxa are parasites and are included as predators.
5. Diptera pupae designations are based on Chironomidae, as majority of pupae were suspected but unconfirmed Chironomidae.
6. These taxa are univoltine/semivoltine (Merritt and Cummins 1996) and are therefore not considered long-lived.